

**Role of Landscape Composition and Geographical Location on Breeding Philopatry in
Grassland Passerines: A Stable Isotope Approach**

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By

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ABSTRACT

Grassland bird populations in North America are in steady decline. Despite declining faster and more consistently than any other group of birds, grassland songbird populations are relatively understudied and little is known about factors driving breeding-site philopatry and dispersal. Landscape and habitat composition may influence fidelity of grassland songbirds to a breeding area. As predicted by the theory of the *Ideal Free Distribution*, high-quality sites are likely to have a higher percentage of return breeders than low-quality sites because higher quality sites should have more or better-quality resources birds need for improved fitness. Using stable hydrogen isotope (δD) analysis, I approximated minimum fidelity rates of two grassland songbirds to two landscape (grass- vs crop-dominated landscapes) and two habitat (native grass vs planted grass) types. I hypothesized that grassland songbirds would return more readily to higher quality sites. For Sprague's Pipit (*Anthus spragueii*), a habitat specialist, this would mean returning more readily to native grass habitat in grass dominated landscapes. I expected no difference in return rate of Savannah Sparrow (*Passerculus sandwichensis*), a habitat generalist, to either habitat or landscape. However, I found that the proportion of non-returning breeders was not influenced by landscape or habitat for either species. Furthermore, I examined attributes (distance from capture point to nearest crop and to the nearest road, as well as the percentage of native grass, planted grass, water and woody vegetation within landscape and territory buffers around the capture point) of the landscape and territory of each individual to determine if specific landscape or territory characteristics influenced their return rate to a breeding area. Neither species showed an affinity or aversion to any of the landscape or territory characteristics considered.

At a larger scale, geographical position within the breeding range may influence dispersal rates of migratory songbirds. Given that environmental factors often change in a clinal manner,

central populations presumably experience the most favorable environmental conditions and peripheral populations the least favorable. Therefore, geographically peripheral locations likely occur in ecologically marginal or stressful conditions, resulting in higher dispersal rates of migratory birds. I examined the differences in dispersal rates of two grassland songbirds at two geographically distinct locations; one centrally located in the Sprague's Pipit breeding range (Last Mountain Lake area, SK, Canada) and one at the periphery (Bowdoin National Wildlife Refuge, MT, USA). As expected, Sprague's Pipits at the Bowdoin National Wildlife Refuge had a significantly larger dispersal rate than at the Last Mountain Lake area. Savannah Sparrow dispersal rates did not differ between locations at the more conservative outlier classification. These results provide some limited evidence that geographical position within the breeding range can influence dispersal rates.

Using δD analysis, I found that local amount-weighted growing-season deuterium in precipitation (δD_p) at locations within grassland ecosystems differed from those long-term (45+ year) models described by stable hydrogen isotope ratio basemaps, illustrated in Hobson and Wassenaar (1997), Meehan et al. (2004) and Bowen et al. (2005). Therefore, I describe how δD_p values were corrected from the long-term isoscape value predicted by Bowen et al. (2005). This method of determining year-specific local weighted growing-season δD_p is an improvement upon the currently used Bowen et al. (2005) isoscape that is based on long-term precipitation patterns. To improve assignment of individuals to origins based on their δD_f values, future research should incorporate year-to-year variation by applying year-specific corrections to the Bowen et al. (2005) isoscape.

More research is needed to determine the factors affecting the philopatry and dispersal of grassland songbirds in order to conserve them.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Dispersal Patterns in Passerines

The geographic distribution and population structure of many migratory passerines is apparently characterized by strong adult breeding-site philopatry and low natal philopatry (Greenwood 1980, Greenwood and Harvey 1982, Sedgwick 2004). Philopatry refers to the tendency of an individual to return to, or stay in, its home area or place of birth. Natal philopatry is the tendency of a second-year individual to return to its place of birth, whereas breeding philopatry is the tendency of an individual to return to the location of breeding the previous year. Both breeding and natal philopatry influence population dynamics and demography (Brown and Kodric-Brown 1977, Freemark et al. 1995, Wheel Wright and Mauck 1998) and may play a role in how population growth or decline is affected by variation in habitat quality. Source-sink dynamics (Lande and Barrowclough 1987, Pulliam 1988, Payne 1991), where populations with negative growth rates (“sinks”) persist through immigration from populations with positive growth rates (“sources”), are usually correlated with habitat quality. Low-quality habitats typically act as “sinks” and high-quality habitats act as “sources”.

Although return rates of birds to breeding grounds may reflect overwinter survival (Askenmo 1979, Weatherhead and Boak 1986, Nol and Smith 1987), it is generally thought that individuals disperse from breeding sites by choice and base their decisions on previous breeding performance (Darley et al. 1977, Gavin and Bollinger 1988, Beheler et al. 2003). Successful breeders likely increase their fitness by returning to a site of known previous success, while unsuccessful breeders may disperse in search of better breeding sites to increase their fitness (Sedgwick 2004). Both Haas (1998) and Hoover (2003) have demonstrated links between breeding success in songbirds and return rates experimentally, such that unsuccessful breeders have lower return rates than successful breeders.

Site quality may influence return rates of individuals. As predicted by the *Ideal Free Distribution* theory (Fretwell and Lucas 1970), high-quality sites likely have a higher percentage of return breeders than low-quality sites because higher-quality sites should have more and better-quality resources birds need for improved fitness. Bollinger and Gavin (1989) demonstrated that breeding ground return rates of Bobolinks (*Dolichonyx oryzivorus*) were similar for successful and unsuccessful breeders on high-quality sites, but unsuccessful breeders were less likely to return to low-quality sites. Return rates may also be influenced by age or gender of the individual. Older birds typically have higher return rates than younger birds (McCleery and Perrins 1989, Badyaev and Faust 1996, Lozano and Lemon 1999) and breeding-site fidelity is often greater in males than in females (Greenwood 1980). Furthermore, competition between individuals for territories may result in socially dominant individuals acquiring territories in higher quality habitat than their subordinates, as predicted by the *Ideal Dominance Distribution Model* (Fretwell and Lucas 1970). Socially dominant individuals may be older individuals, healthier individuals or returning breeders who have prior knowledge of the area, allowing them to successfully compete for resources over newcomers.

Little is known about dispersal and breeding-site philopatry in songbirds due to the difficulty in tracking using conventional mark-recapture methods. Millions of birds have been banded to better understand migratory connectivity. Although this is a successful method of acquiring information on movement of game birds, it has not been as successful for migrant songbirds due to low recapture rates (Hobson 2003). Although radio and satellite transmitters give accurate location information, these methods are very expensive and currently have weight and size constraints that limit their use on small passerines. These limitations have resulted in an increased interest in using intrinsic markers such as population-level genetic markers, stable

isotopes, and trace-element profiles in tissues (Hobson 2005, Hobson and Norris 2008), despite reduced resolution of the location information gathered relative to other conventional mark-recapture methods. The main benefit to using intrinsic markers is that information on origins can be obtained without the bias and cost associated with mark-recapture techniques. Given that each individual carries information regarding previous origins, every capture is essentially a recapture (Royle and Rubenstein 2004, Hobson 2005).

1.2 Using Stable Isotopes to Detect Origins and Dispersal

1.2.1 General Information

Stable isotope analysis can offer an effective way of tracking migratory songbirds and is becoming an increasingly important tool for avian biologists. The stable isotope abundance of any element is typically expressed as a ratio of the rarer, heavy form to the common, lighter form. This ratio is reported in delta notation (δ) according to the following equation (Ehleringer and Rundel 1989):

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (1.1)$$

where X is the heavy isotope, R_{sample} is the heavy to light isotope ratio of the sample and R_{standard} is the heavy to light isotope ratio of the standard. The isotopic standard used for hydrogen is Vienna Standard Mean Ocean Water (VSMOW).

Biogeochemical processes in nature result in varying stable isotope abundances of materials and these differences allow one to infer origins of organisms that rely on these materials and equilibrate with the local foodwebs (Hobson 2005). This phenomenon is based on the relationship that an organism's tissues reflect its diet and can be expressed as follows:

$$\delta X_t = \delta X_d + \delta \Delta_{dt} \quad (1.2)$$

where X is the heavy isotope of interest, t is the tissue measured, d is the diet and Δ_{dt} is the isotopic discrimination factor between the diet and the tissue.

Assimilation of elements by animals, primarily through diet, results in naturally occurring isotopic markers within the organisms' tissues that can be used to estimate location of tissue growth (Estep and Dabrowski 1980). Although applicable to metabolically active tissues, this is particularly useful when the tissue in question is inert following synthesis because the isotopic composition of the tissue reflects the diet during the period of growth only (Hobson and Clark 1992). Feathers are useful markers because they are metabolically inert following synthesis.

1.2.2 Hydrogen Isotope Theory

One element that is of great interest to ecologists is hydrogen. Hydrogen has two naturally occurring stable isotopes: deuterium (^2H , δD) and protium (^1H). Precipitation amount-weighted average δD (herein δD_p) has a characteristic geographic pattern across North America. The δD_p decreases as moist air masses travel from low to high latitudes, from low to high altitudes, and from the coasts to inland portions of the continent (Dansgaard 1964) by a process known as Rayleigh distillation. Rayleigh distillation, or the selection against heavy isotopes during evaporation and condensation, results in a continent-wide pattern with a general gradient from enriched values (more deuterium and therefore more positive δD values relative to the standard) in the southeast to more depleted values in the northwest (Sheppard et al. 1969, Taylor 1974, Hobson and Wassenaar 1997). Generally, precipitation at the base of mountains or along coastlines is enriched in deuterium because deuterium in precipitation rains out at lower

elevations and along coastlines (Dansgaard 1961, Zeigler 1988). Isotopic patterns may also vary among years, particularly during El Nino and La Nina years. Previous studies have determined there is a strong correlation between the δD values of environmental water and those in plant biomass (Yapp and Epstein 1982). Estep and Dabrowski (1980) found that these patterns were also passed on to organisms at higher trophic levels. The relative abundance of δD in local food webs is expressed in animals that fix those isotopic values in tissues grown at those locations (Cormie et al. 1994a). The δD_p during the growing-season (δD_{p-gs}) is closely correlated with the δD values in bird feathers (δD_f). It is this relationship that allows researchers to track origins of migratory species (Chamberlain et al. 1997, Hobson and Wassenaar 1997).

Two issues that researchers must be aware of when using stable hydrogen isotope analysis are the isotopic discrimination factor and exchangeability. The discrimination factor is a result of a process known as fractionation. Fractionation is a chemical reaction or physical process that causes a relative change in the proportions of different isotopes of the same element in various compounds. Isotopes of an element may have slightly different equilibrium constants for a particular chemical reaction, so that slightly different amounts of reaction products are made from reactants containing different isotopes. This leads to isotopic fractionation, the extent of which is known as the discrimination factor. Fractionation causes the difference between the stable hydrogen isotope ratio in the diet and the stable hydrogen isotope ratio in the tissue. For feathers, this discrimination factor is approximately -25‰ (Wassenaar and Hobson 2000, Hobson et al. 2004, Hobson 2005). Exchangeability is the degree to which uncontrolled hydrogen isotopic exchange between “exchangeable” organic hydrogen in tissues and isotopically variable ambient moisture in the laboratory environment occurs (Wassenaar and Hobson 2003) via a chemical reaction in which a covalently bonded hydrogen atom (H-N, H-O)

is replaced by a deuterium atom or vice versa. This can be problematic if left uncorrected, as the δD value of the total hydrogen in an identical feather will yield different results at laboratories located at different geographic locations and at different times of the year due to geographical and seasonal changes in the hydrogen isotopic composition of the ambient moisture (Wassenaar and Hobson 2003). This phenomenon must be accounted for to make measurements comparable among varying times and locations.

At the National Hydrology Research Centre, all feather samples are compared to previously (steam) calibrated keratin working standards. These working standards have similar chemical and exchangeable hydrogen properties as the feathers. In the case of δD , three keratin working standards are used; chicken feather (CFS: -147.4‰), cow hoof (CHS: -187‰) and bowhead whale baleen (BWB-II: -108‰). Each standard was collected from a single geographic location and represents both terrestrial and marine environments, allowing for a wide range of δD values to be compared (Wassenaar and Hobson 2003). Prior to δD analysis, samples and keratin standards are allowed to “air equilibrate” on a shelf with ambient lab air moisture at room temperature for >96 hours (Wassenaar and Hobson 2003). Following this comparative equilibration, all samples and standards are loaded into the auto sampler carousel of the online continuous-flow isotope-ratio mass spectrometer and analyzed for δD . Both the discrimination factor between the δD in precipitation and feather tissue and exchangeability were accounted for in this study.

In summary, this approach relies on the fact that isotopic values of the foodweb are reflected in an organism’s tissue and that such values can vary spatially based on a variety of biogeochemical processes (Hobson 1999). When organisms move between isotopically distinct foodwebs, they carry with them information on the previous feeding location (Hobson 1999).

Most species of migrant songbirds grow their flight feathers on or near the breeding grounds (Pyle 1997) allowing the approximate latitude of their breeding grounds to be determined using stable hydrogen isotope analysis of the flight feathers (Hobson 1999, Figure 1.1).

1.2.3 Assignment of Individuals

Stable hydrogen isotope analysis has the potential to be a very useful tool in determining breeding dispersal of migratory birds and allows one to determine if an individual grew its feathers in the region as the previous year and one can therefore separate returning breeders from non-returning (herein outlier) breeders. However, for this to be effective, it is important to be able to reliably assign the individual to the correct region of feather growth. Reliably assigning individuals to molt origin relies on a few key principles of assignment (Wunder and Norris 2008). It is essential that detectable and predictable patterns (or at least differences) exist in the spatial distributions of stable isotopes in the environment from where migratory organisms feed. Furthermore, these patterns in the environment must be faithfully maintained as they are translated through the food web. This means that the discrimination factor between stable isotopes in the diet and the tissues of interest must be predictable and constant over time and space. Finally, models for assigning individuals to locations are critically dependent on assign-time calibrations (Wunder and Norris 2008), or the use of known-location tissues to relate isotope values to geography and environmental material. These “standards” (i.e. tissues of known geographic origin) are most accurate when a tissue with similar chemical compositions to that of the unknown samples is used. Geographic assignment models perform best when calibrated “standards” are from the same species and encompass the same isotopic range (both within time and space) as the unknown samples.

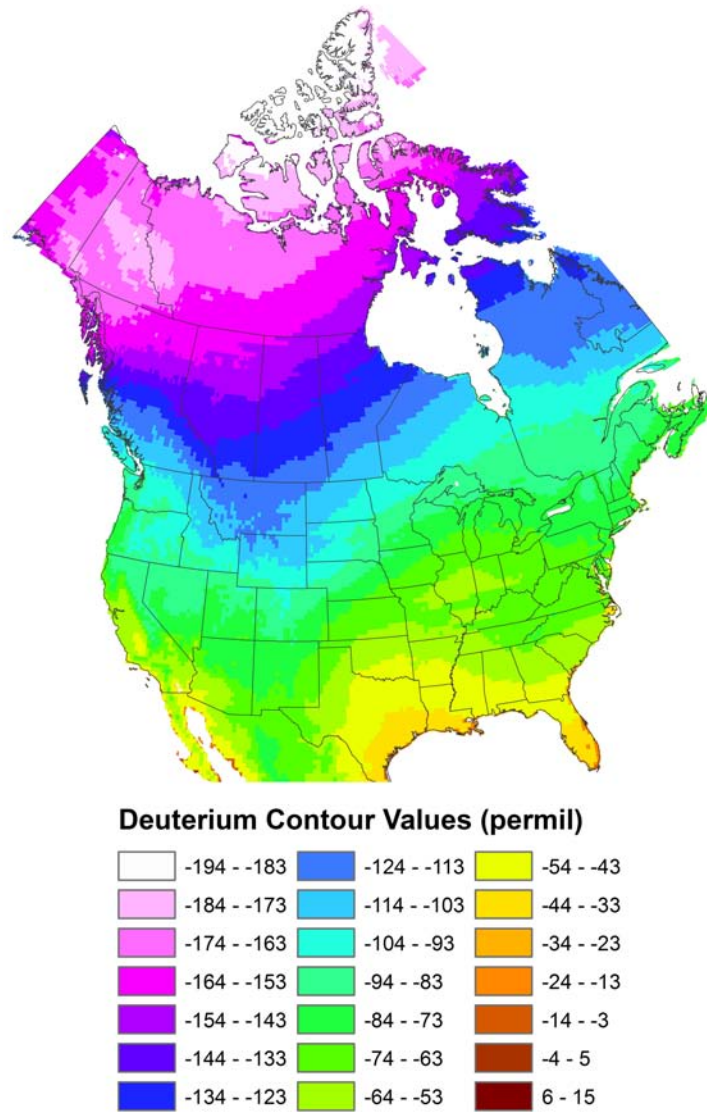


Figure 1.1. Feather deuterium (δD) contours in North America depict a continent-wide pattern of more enriched δD values in the southeast to more depleted values in the northwest. Figure was constructed using the Bowen et al. (2005) isoscape and correcting precipitation deuterium values by -25‰ to depict feather deuterium values.

Although many studies have used δD analysis to look at movement of animals in various taxa (Cryan et al. 2004, Rubenstein and Hobson 2004), few studies have used δD analysis to look at dispersal in birds. Hobson et al. (2004) used stable isotopes to determine dispersal of American Redstarts (*Setophaga ruticilla*) and Ovenbirds (*Seiurus aurocapillus*). In that study, individuals were classified as outliers using box and whisker plots. Individuals outside the whisker limit (defined as 1.5 times the length of the box defining the 25% and 75% quartiles) were considered outliers. That approach assumed that most of the birds in the populations were local and that the mean feather δD value for the population resembled that expected for the location. Hobson (2005) suggests a more ideal approach to using stable isotopes to detect dispersers would be to create the expected isotopic distribution of stable isotope profiles of local individuals based on conventional marking studies. Perez and Hobson (2007) defined a resident Loggerhead Shrike (*Lanius ludovicianus*) as an individual that had δD_f values within a range of values, based on Lott and Smith (2006) or museum samples. All other individuals were classified as migrants. I chose to define dispersing birds as those that fell outside the range of a “local bird”. A “local bird” was defined as an individual that fell within a range of values ($\pm 6\text{‰}$ or $\pm 10\text{‰}$) around a site-specific estimated δD_f value. A local bird in this case is one that may still be an outsider or dispersing bird, but which has the same range of isotope values as a true returning breeder. With this conservative approach, I can identify true outsider birds, but the designation of a true returning breeder will always be problematic.

There are several methods of determining the expected local feather deuterium value of a location as a way of assigning an individual of unknown origin to a geographical area during a previous period of the migratory cycle.

1.2.3.1 Use of Mean Observed Feather Value

The simplest way to determine an expected local feather deuterium value is to take the mean observed feather deuterium value of all individuals collected from that location. The assumption is that the species of interest is highly philopatric and individuals caught at the location are likely to be returning breeders. This is a crude method of determining an expected local feather deuterium value, but may be the best choice when unable to rely on any of the other methods.

1.2.3.2 Map Lookup Approach

The “map lookup” approach (Wunder and Norris 2008) involves defining geographic gradients (basemaps) of isotope values, measuring the δD_f of an individual of unknown origin, and then assigning it to the area of the mapped gradient that corresponds to its isotope value. These maps of isotopic δD_p values (or isoscapes) are typically generated from the spatial patterns in δD caused by indirect sources (e.g. rainfall) and then converted to δD_f values using a regression between δD_f of songbirds and the predicted δD values in growing-season precipitation at sampling locations across North America described in Clark et al. (2006). However, there are many sources of variability associated with δD_p values and isoscapes need to be calibrated to account for that variation. Ideally, isoscapes of δD_f will be calibrated for each species using known origin tissues (gathered from the same species, age class, habitats and years as the samples of interest) that were collected from across the full extent of the geographic range of the species. However, in most cases, these data are unavailable. Therefore, the next best approach would be to use published calibrations between δD_f and δD_p values that correspond most closely to the species and geographic range of interest. Once a calibrated isoscape has been developed, individuals can be assigned to the isoscape. Individuals can be assigned to a specific region (i.e.

the specific region on the mapped gradient that corresponds to the isotope value of the individual) or to an extensive area (i.e. a large area defined by a range of isotope values).

1.2.3.3 Use of Deuterium in Local Precipitation

The local growing-season average deuterium value in precipitation at a site can be used in conjunction with the regression analysis described by Clark et al. (2006) to determine the expected δD_f for a specific site. The Clark et al. (2006) regression analysis between δD_f of songbirds and the predicted precipitation amount-weighted δD values in growing-season precipitation at sampling locations across North America describes the change in deuterium from precipitation thru the food chain and into feathers. This results in a deuterium value that represents the expected δD_f of a feather grown at that location. The local amount-weighted growing-season average deuterium value in precipitation (δD_w) is calculated using the following equation (Hobson and Wassenaar 1997):

$$\delta D_w = \frac{\sum_{i=1}^n (X_i * \delta D_i)}{\sum_{i=1}^n X_i} \quad (1.3)$$

where δD_i is the average deuterium value (‰) in precipitation collected for the month i and X_i is the amount of precipitation (mm) during the month. Growing season is defined as those months where the average monthly temperature is $> 0^\circ\text{C}$ prior to molt. Growing-season precipitation is used instead of annual precipitation because grassland vegetation responds more readily to short-term rainfall events (Sala and Lauenroth 1982) and therefore, the deuterium values that birds incorporate in their tissues will reflect the growing season.

1.2.3.4 Probability Assignment Method

Recently, assignment of birds to geographic origin has been done using likelihood-based assignment tests (Wunder et al. 2005, Norris et al. 2006). These more rigorous statistical techniques assign birds to geographic zones of origin by determining the probability that an individual originated from any given region. Baye's Rule can be used to calculate the probability an individual originated from a particular region given the measured δD_f and a specified distribution of errors (Royle and Rubenstein 2004). Probability surfaces can then be created to represent the probability that any point in space is the true origin of an individual for which stable isotope values are measured (Wunder and Norris 2008). Assignment of birds to geographic origin can be further refined by incorporating prior information (e.g. abundance data). In this case, if an individual had an equal probability of being assigned to either of two regions based on the isotopic values, but one region had much greater abundance of the species of interest, then probability theory would suggest that based on random chance, the region with higher abundance would represent the more likely origin. These methods are computationally intensive and have yet to be used to classify an individual as an outlier or non-returning breeder. However, these methods do have potential for use in studies of dispersal.

1.2.3.5 Use of Recaptured Individuals

Quantifying the deuterium value in feathers of recaptured individuals gives the best estimate of the expected local feather deuterium value. In this case, the location of origin, as well as the feather deuterium value for that location, is known. This allows assignment of individuals of unknown origin with similar feather deuterium values to be assigned to that region quite reliably. This method is species-specific, which improves its reliability to correctly assign individuals of that species. However, despite being the most reliable method of assignment, it is difficult to

recapture individuals in subsequent years, particularly for grassland passerines (Jones et al. 2007).

1.3 Grassland Passerines

Grassland bird populations are declining faster and more consistently than any other group of North American birds (Sauer et al. 2005, Downes and Collins 2007). Although conversion of grassland habitat to cropland has likely been a main contributor to this decline (Peterjohn and Sauer 1999), habitat degradation and fragmentation may also be compounding the problem (Brennan and Kuvlesky 2005). Habitat degradation and fragmentation may limit the availability of optimum habitat for reproduction and force birds to attempt reproduction in lower-quality habitats (Fretwell and Lucas 1970). If these lower-quality habitats cannot provide the components necessary for successful reproduction, then population declines may occur if immigration to the area cannot offset mortality and emigration.

Landscape structure and composition have been identified as factors affecting occurrence of grassland songbirds (e.g. Ribic and Sample 2001, Bakker et al. 2002, Cunningham and Johnson 2006, Koper and Schmiegelow 2006) and they may also affect breeding-site philopatry and dispersal. This is the first study to use stable hydrogen isotope analysis to assess breeding philopatry as it relates to landscape and habitat composition. Furthermore, this is the first study to use this technique to investigate large scale differences in dispersal rates of grassland songbirds. Insights into how birds perceive grassland habitats at various spatial scales and how this influences the likelihood that they settle or return to these areas will allow conservation planners to protect habitats with high rates of philopatry and presumably greater fitness.

1.4 Study Species

Sprague's Pipit (*Anthus spragueii*) is a threatened ground-nesting passerine that is endemic to the Northern Mixed-grass Prairie (Mengel 1970) during the breeding season. This species breeds from southern and central Alberta, to west-central and southern Manitoba, and south to central Montana, northern South Dakota and northwestern Minnesota (Robbins and Dale 1999). Most individuals arrive on the breeding grounds in late April, early May, and depart for the wintering grounds by late September (Robbins and Dale 1999). The Sprague's Pipit wintering range consists of the southern United States and the northern two-thirds of Mexico (Robbins and Dale 1999). Although still relatively common in areas with suitable habitat, populations in Alberta and Saskatchewan have declined by 6.0% and 4.9% per year respectively since 1968 (Downes and Collins 2007).

Numerous studies have suggested that Sprague's Pipit is strongly associated with native grasslands (Prescott and Davis 2000), preferring well-drained areas in open grassland (Robbins and Dale 1999) with vegetation of moderate height and density and few shrubs or trees (Sutter et al. 2000, Grant et al. 2004). Furthermore, it is an area-sensitive species and is most abundant on larger tracts of contiguous prairie (Davis 2004, Davis et al. 2006). Sprague's Pipit is highly sensitive to anthropogenic changes in its breeding habitat and is a good indicator of grassland quality in the Canadian prairies (Prescott and Davis 2000). Although the degree of philopatry to breeding sites has not been studied for this species, recapture of several banded individuals suggest that this species exhibits some level of breeding-site fidelity in northern Montana (Jones et al. 2007) and south-central Saskatchewan (S. Davis, unpublished data).

Savannah Sparrows (*Passerculus sandwichensis*) breed throughout Canada and the United States, ranging from Alaska and the Canadian territories to coastal southern California, northern New Mexico and the Great Lakes region (Wheelwright and Rising 1993). The species winters in

the southern United States, Guatemala, Belize, throughout most of Mexico, and on various islands in the Caribbean (Wheelwright and Rising 1993).

In contrast to Sprague's Pipit, the Savannah Sparrow is commonly found in both native and non-native grassland habitats (Davis and Duncan 1999, McMaster and Davis 2001) and is considered to be a grassland habitat generalist (Wheelwright and Rising 1993). Savannah Sparrows avoid grasslands with trees (Grant et al. 2004, Wheelwright and Rising 1993), but are not generally sensitive to habitat patch-size (Johnson and Igl 2001, Davis 2004, but see Bakker et al. 2002, Winter et al. 2006) and exhibit a high degree of site fidelity (Bédard and LaPointe, 1984).

These species were good candidates for δD analysis because both molt their primary flight feathers on the breeding grounds. Therefore, the primary flight feathers have a δD_f value that is indicative of the breeding ground, which allows researchers to assign individuals to the previous years' breeding grounds when captured. Furthermore, both species migrate within North America, as opposed to species which migrate to South America, allowing researchers to correlate δD_f values to the precipitation contours of deuterium established for North America.

Initially Baird's Sparrow (*Ammodramus baridii*) was also included in this study. Baird's Sparrows are ground nesting passerines that are endemic to the Northern Great Plains. Baird's Sparrows breed from the southern portions of the Prairie Provinces (Alberta, Saskatchewan and Manitoba) south to central and eastern Montana, northwestern North Dakota and north-central South Dakota (Green et al. 2002). It primarily winters in northern Mexico, but is also found in the southern United States (Green et al. 2002). Baird's Sparrow is a habitat specialist and is found in mostly native grassland habitats (Sutter et al. 2000, McMaster et al. 2005) but also inhabits planted grassland (Davis et al. 1999, Davis and Duncan 1999). The species is associated

with vegetation of intermediate height and density (Sutter et al. 2000) and avoids trees and shrubs (Grant et al. 2004, Davis 2005). Johnson & Igl (2001) and Davis (2004) report that Baird's Sparrows are area sensitive in some portions of their range. The philopatry of this species is unknown, but recapture of banded individuals suggests some level of breeding-site fidelity (Jones et al. 2007, S. Davis , unpublished data).

I omitted this species from the study because the distribution of observed feather deuterium values of the first primary (P1) indicated that Baird's Sparrows do not always molt their P1 on the breeding grounds (Appendix A, Figure A.1), which is further supported by Voelker (2004). Therefore, I could not reliably determine the location of the previous year's breeding ground.

1.5 Thesis Objectives and Organization

The general objectives of my thesis were as follows:

1. To determine the degree to which habitat and landscape composition influences the breeding-site fidelity of Sprague's Pipit and Savannah Sparrow.

I predicted that higher-quality habitats and landscapes would show a larger proportion of returning breeders and fewer new recruits from elsewhere. I predicted Sprague's Pipit, a native grassland specialist, would prefer habitats and landscapes with a higher proportion of native grassland. Subsequently, these sites should have a greater proportion of birds returning to breed. I predicted Savannah Sparrow, a grassland habitat generalist, would show no preference between habitat and landscape types. To do this, I used stable hydrogen isotope analysis to classify after-hatch-year birds as a returning or non-returning breeder and related it to the habitat and landscape composition of the individual's 2006 breeding location.

2. To determine whether philopatry to breeding sites was greater in the center or periphery of the breeding range of two grassland passerines.

I hypothesized that geographically peripheral locations would experience higher dispersal rates. I predicted there would be a smaller proportion of returning Sprague's Pipit breeders in northern Montana given that this location is at the south-western edge of their breeding range. I expected the proportion of returning Savannah Sparrow breeders would be similar between Last Mountain Lake, SK and the Bowdoin National Wildlife Refuge, MT, as both are near the center of their breeding range. I used stable hydrogen isotope analysis to classify individuals as returning or non-returning breeders and estimated the proportion of returning breeders at each location.

I organized my thesis into four chapters. Chapters 1 and 4 are the General Introduction and Summary and Synthesis, respectively. Chapter 2, *Influence of habitat type and landscape composition on breeding philopatry and dispersal of grassland passerines: A stable hydrogen isotope (δD) approach*, addresses objective 1 and focuses on the role landscape and habitat composition plays in the breeding-site philopatry of Sprague's Pipit and Savannah Sparrow. Chapter 3, *Role of geographical location on breeding dispersal of grassland passerines: A stable hydrogen isotope (δD) approach*, addresses objective 2 and focuses on the large-scale differences in dispersal at a central and a peripheral location within the Sprague's Pipit breeding range. Both chapter 2 and 3 are structured as scientific journal articles. Appendices A, B and D present supplemental tables for chapter 1, 2 and 3, respectively. Appendix C, *Deriving year- and*

site-specific feather δD isoscapes to assign migratory birds to origin, describes an improved method of assigning individuals to a location of origin.

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CHAPTER 2: INFLUENCE OF HABITAT TYPE AND LANDSCAPE COMPOSITION ON BREEDING PHILOPATRY AND DISPERSAL OF GRASSLAND PASSERINES: A STABLE HYDROGEN ISOTOPE (δD) APPROACH

2.1 Abstract

Landscape and habitat composition may influence fidelity of grassland songbirds to a breeding area. High-quality sites are likely to have a higher percentage of return breeders than low-quality sites because higher quality sites should have more or higher-quality resources birds need for improved fitness. I used stable hydrogen isotope analysis to determine the fidelity of grassland songbirds to two landscape (grass- vs crop-dominated landscapes) and two habitat (native grassland vs planted grassland) types. I hypothesized that grassland birds would return more readily to higher-quality sites. Higher-quality sites were assumed to have sufficient resources for improved fitness. Habitat correlates of improved fitness were based on knowledge of species' life-history traits. For Sprague's Pipit (*Anthus spragueii*), a native grassland specialist, I expected a higher proportion of returning breeders to native grass habitat in grass-dominated landscapes. Since the Savannah Sparrow (*Passerculus sandwichensis*) is a habitat generalist, I expected no difference in return rate to either habitat or landscape. Using stable hydrogen isotope analysis, I determined the proportion of non-returning breeders on each landscape and habitat type. The proportion of non-returning breeders, defined as those individuals with a feather deuterium value outside the range of values expected for a local bird, did not significantly differ on either landscape or habitat for either Sprague's Pipit or Savannah Sparrow. Furthermore, I examined distance from capture point to nearest crop and to the nearest road, as well as the percentage of native grass, planted grass, water, and woody vegetative material within the landscape and territory of each individual to determine if these attributes influenced the return rate to a breeding area. Neither species showed an affinity or aversion to any of the landscape or territory characteristics considered. Contrary to expectations, Sprague's

Pipits and Savannah Sparrows did not respond to the landscape and territory characteristics I defined

2.2 Introduction

2.2.1 Grassland Bird Conservation

Grasslands are among the most threatened ecosystems in North America (Samson and Knopf, 1994). The Northern Mixed-grass Prairie has declined by 72-99% across the United States (Samson and Knopf 1994). Only 24% of the original Mixed-grass Prairie remains in Canada (Environment Canada 2007) and only 20% in Saskatchewan (Hammermeister et al. 2001). Extant native prairie throughout the Great Plains continues to be lost or degraded by cultivation, invasion of exotic plant species and woody vegetation, over-grazing, and urban development (Samson and Knopf 1994, Riemer et al. 1997). This loss is believed to have caused grassland birds to also undergo drastic and widespread declines (Peterjohn and Sauer 1999, Brennan and Kuvlesky 2005). Insights into how grassland birds perceive grassland habitats at various spatial scales and how this influences the likelihood that they settle or return to these areas would enhance our ability to direct grassland songbird conservation towards habitats that grassland birds are likely to settle in or return to (Bakker et al. 2002).

2.2.2 Breeding Dispersal

Breeding dispersal (the tendency for adults to disperse from their site of previous breeding) in birds is thought to be a response to ecological and social conditions on the breeding grounds to optimize individual fitness (Pasinelli et al. 2007). Several hypotheses have been proposed to explain when breeding dispersal should occur. The *reproductive hypothesis* states that individuals may use their own reproductive performance or the reproductive performance of

conspecifics to assess whether they should disperse from a site (Gavin and Bollinger 1989, Forero et al. 1999, Sedgwick 2004). In this scenario, low breeding success of the individual or their conspecifics would result in birds dispersing from the area. The *social constraints hypothesis* contends that individuals disperse in response to intraspecific competition (Payne and Payne 1993, Otter and Ratcliffe 1996). For example, breeding dispersal has been found to be positively correlated with the density of conspecifics (Pasinelli et al. 2007). The *predation risk hypothesis* states that nest predation influences breeding dispersal (Haas 1998). Accordingly, territories are chosen that reduce predation risk (Pasinelli et al. 2007). Lastly, the *site choice hypothesis* states that individuals will disperse to improve the quality of their breeding site (e.g. Bollinger and Gavin 1989, Korpimäki 1993, Stanback and Rockwell 2003). Territory quality, defined as the availability of habitat variables important to the foraging habitat and quality of the nest site, has been shown to influence local recruitment, such that recruitment increases with increasing territory quality to some optimal level (Pasinelli et al. 2007). Therefore, the probability of breeding dispersal is expected to be negatively correlated with the quality of territories held in the year prior to dispersal (Pasinelli et al. 2007).

2.2.3 Rationale and Objectives

Using stable hydrogen isotope analysis, I identified birds that had undergone long-distance north-south dispersal and thus an individual's fidelity to or dispersal from different quality habitats. Sprague's Pipit (*Anthus spragueii*) and Savannah Sparrow (*Passerculus sandwichensis*) are appropriate species to study because they breed throughout a clear latitudinal hydrogen isotopic gradient in North America. Breeding-site fidelity of most grassland passerines has not been studied due to problems with conventional mark-recapture methods (Hobson 2005). My objective was to determine the degree to which habitat and landscape composition influenced the

breeding-site fidelity of Sprague's Pipit and Savannah Sparrow in south-central Saskatchewan. I hypothesized that higher quality habitats and landscapes would show a larger proportion of returning breeders.

Habitat specialist and generalist species are both likely to return to high-quality habitats. However, habitat generalists are more likely to experience higher reproductive success in lower-quality habitats because they may be better adapted to varying habitats. As a result, habitat specialists may be more likely to disperse from a lower-quality habitat than habitat generalist species. In this study, I considered habitats and landscapes with a higher proportion of native grassland to be high-quality habitats. Therefore, I predicted Sprague's Pipit, a grassland specialist, would exhibit greater levels of fidelity to habitats and landscapes with a higher proportion of native grassland. I expected the difference in Savannah Sparrow fidelity to high- and low-quality habitats to be less than that of Sprague's Pipit because Savannah Sparrow is a grassland generalist.

2.3 Methods and Study Design

2.3.1 Study Site

Field work was conducted at the north end of Last Mountain Lake, Saskatchewan, Canada (51° 20' N, 105° 15' W) from May 1st to July 31st, 2006. This area is a mosaic of native grassland, planted grassland (hay fields and pasture), and cropland. The surrounding area is primarily used for agriculture, such as annual cropping, haying and ranching (Appendix B, Figure B.1).

2.3.2 Study Species

Sprague's Pipit is a threatened (Environment Canada 2008) ground-nesting passerine that is endemic to the Northern Mixed-grass Prairie (Mengel 1970). This species breeds from southern

and central Alberta, to southwestern Manitoba, and south to central Montana, northern South Dakota and northwestern Minnesota (Robbins and Dale 1999, see Appendix B, Figure B.2). Most individuals arrive on the breeding grounds in late April, early May, and depart for the wintering grounds by late September (Robbins and Dale 1999). Although still relatively common in areas with suitable habitat, populations in Alberta and Saskatchewan have declined by 6.0% and 4.9% per year, respectively, since 1968 (Downes and Collins 2007).

Numerous studies have suggested that Sprague's Pipit is strongly associated with native grasslands (Prescott and Davis 2000), preferring well-drained areas in open grassland (Robbins and Dale 1999) with moderate grass height and density and few shrubs or trees (Madden et al. 2000, Grant et al. 2004). Furthermore, it is an area-sensitive species and is most abundant on larger tracts of contiguous prairie (Davis 2004, Davis et al. 2006). Sprague's Pipit is highly sensitive to anthropogenic changes in its breeding habitat and is a good indicator of grassland quality in the Canadian prairies (Prescott and Davis 2000). Although the degree of philopatry to breeding sites has not been studied for this species, recapture of several banded individuals suggest that this species exhibits breeding-site fidelity to Last Mountain Lake, SK (S. Davis, unpublished data) and Bowdoin National Wildlife Refuge, MT (Jones et al. 2007).

Savannah Sparrow breeds throughout Canada and the United States, ranging from Alaska and the Canadian territories to coastal southern California, northern New Mexico and the Great Lakes region (Wheelwright and Rising 1993, see Appendix B, Figure B.3). It winters in the southern United States, Guatemala, Belize, throughout most of Mexico, and on various islands in the Caribbean (Wheelwright and Rising 1993).

In contrast to Sprague's Pipit, Savannah Sparrow is commonly found in both native and non-native grassland habitats (Davis and Duncan 1999, McMaster and Davis 2001) and is considered

a grassland habitat generalist, being found in grassy meadows, cultivated fields, hay fields, lightly grazed pastures, roadsides, coastal grasslands, sedge bogs, edges of salt marshes and tundra (Wheelwright and Rising 1993). Savannah Sparrows avoid grasslands with trees (Grant et al. 2004, Wheelwright and Rising 1993), but are not generally sensitive to habitat patch-size (Johnson and Igl 2001, Davis 2004, but see Bakker et al. 2002, Winter et al. 2006) and exhibit a high degree of site fidelity (Bédard and LaPointe, 1984).

2.3.3 Study Site Selection

Potential study sites were initially identified as quarter sections (64 ha) of native or planted grassland according to 1995 South Digital Land Cover Landsat imagery (McTavish 1995). These quarter sections were considered acceptable sites if there was > 50% of the target grass type. Each quarter section was buffered by a radius of 1.6 km and the proportion of grassland quantified within the buffer (including the quarter section). I considered buffered quarter sections to be grass-dominated landscapes if they were composed of > 60% grass and crop-dominated landscapes if < 40% grass. This ensured representation of different habitats under different degrees of cultivation, yet enough grassland habitat to attract the target species. I randomly selected 116 sites from the pool of acceptable quarter sections ($n = 215$) identified above; 37 native grassland sites in grass-dominated landscapes, 32 planted grassland sites in grass-dominated landscapes, 24 native grassland sites in crop-dominated landscapes and 23 planted grassland sites in crop-dominated landscapes. I tried to avoid selecting adjacent sites, although was not always successful. I ground-truthed sites in April, prior to the birds' arrival to verify land use.

2.3.4 Avian Sampling

I captured adults and collected feathers from May through July, 2006. I attempted to capture one individual of each species on each quarter section using playback recordings, a decoy, and two 6 m mist nets. The two 6 m mist nets (mesh size = 30mm x 30mm) were set up in a V-formation with a species-specific decoy placed where the mist nets meet. A digital caller (Western Rivers Predation MP3 game caller, Lexington, TN) was placed next to the decoy and a focal-species specific territorial male song broadcasted. The song was played as long as the bird continued to aggressively defend the territory or until the bird consistently avoided being caught in the nets. Once captured, birds were banded, sexed, aged, measured, and feather samples collected (see below). All birds were banded with a United States Geological Survey (USGS) aluminum band. Birds were sexed according to presence or absence of brood patch and cloacal protuberance (Pyle 1997). Morphological measurements were taken according to Monitoring Avian Productivity and Survivorship (MAPS) protocol (DeSante et al. 2008).

The first primary (P1) and fourth rectrix (R4) were removed, as these feathers are replaced on the previous year's breeding grounds (Pyle 1997). Feathers were pulled, rather than clipped, to initiate re-growth and reduce the duration of impact on flight. Each feather was placed in a labeled paper envelope.

2.3.5 Laboratory Analysis

Feather samples were cleaned of surface oils in 2:1 chloroform:methanol solution overnight, drained and air dried under a fumehood. The middle portion of the feather vane was cut out and $0.35 \text{ mg} \pm 0.02 \text{ mg}$ weighed and placed into 4.0 mm x 3.2 mm silver capsules for online hydrogen isotope analysis by continuous-flow isotope-ratio mass spectrometry (CFIRMS). Stable hydrogen isotope analytical measurements (δD) followed the “comparative equilibration”

technique described by Wassenaar and Hobson (2003). The process involves the measurement of unknowns with several replicates of three different keratin standards whose nonexchangeable δD values are known and which span the range of expected feather values. This provided a way of correcting for uncontrolled isotopic exchange between samples and ambient water vapor (Wassenaar and Hobson 2000, Hobson et al. 2004) so that the values reported are equivalent to nonexchangeable feather hydrogen.

Isotopic values were expressed in delta notation in parts per thousand (‰) as the non-exchangeable hydrogen portion of samples normalized on the Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale. Feather samples were analyzed at the stable-isotope facility of the National Hydrology Research Centre in Saskatoon, Canada.

2.3.6 Local Deuterium Values and Outlier Definition

To determine mean growing-season precipitation δD values for Last Mountain Lake I used interpolated GIS-based models of stable hydrogen isotope ratios in North America derived from growing-season precipitation (See Appendix C). This approach involved using a version of the Bowen et al. (2005) isoscape corrected for annual variation in precipitation to determine the expected weighted average mean growing-season precipitation deuterium value (δD_{p-gs}) for a specific location (i.e. Last Mountain Lake) in a specific year. I converted the δD_{p-gs} value to a feather deuterium value (δD_f) using a regression between δD_{p-gs} and δD_f (Appendix C, Equation C.2). Although a strong relationship exists between δD_{p-gs} and δD_f (Hobson and Wassenaar 1997), the discrimination factor between them varies among taxonomic group (see Wassenaar and Hobson 2001, Bowen et al. 2005, Lott and Smith 2006). I chose to use the relationship between δD_f of songbirds and the predicted δD values in growing-season precipitation at

sampling locations across North America depicted in Clark et al. (2006, Figure 3; see Appendix B, Figure B.4 and Appendix C for more detailed information). This regression is consistent with the discrimination factor of -25‰ determined by Hobson et al. (2004a) work on ovenbirds (*Seiurus aurocapilla*). Langin et al. (2007) also found the discrimination factor to be -25‰ for American redstarts (*Setophaga ruticilla*). By following this procedure, I determined the δD_f value of Last Mountain Lake to be -113‰ in 2005. This value was used for feather comparisons.

I determined an acceptable range of within-bird δD isotopic variation to categorize individual birds as returning (herein non-outlier birds) or non-returning birds (herein outlier birds) to the breeding grounds. Two ranges of variation about the expected mean local feather value were used. I chose $\pm 6\text{‰}$ based on Wassenaar and Hobson (2006) who found that within-feather δD isotopic variance for captive birds was as low as $\pm 3\text{‰}$ for vane material and suggest a more realistic variance to expect is on the order of $\pm 6\text{‰}$. An outlier classification of outside $\pm 10\text{‰}$ of the expected local feather mean was also chosen after reviewing the range of between-feather variation within individual birds captured at Last Mountain Lake in 2006. I compared δD values from the first primary (P1) feather and the fourth rectrix (R4) feather taken from each individual, as both feathers should have been grown on the breeding grounds and therefore should have the same δD_f value. Feather δD values of P1 and R4 were significantly correlated ($r = 0.47$, $p = 0.01$, $n = 50$) and 77% of the birds had P1 and R4 values that were within 10‰ of one another. Feathers with δD values suggesting adventitious replacement by having a δD value outside the breeding range were not considered. At both outlier classifications, a bird would have had to disperse a very long distance for a difference in the isotopic signature to be noticed and consequently to be considered an outlier bird. In the Great Plains of North America, a range of

$\pm 6\text{‰}$ and $\pm 10\text{‰}$ correspond to an estimated north-south range of 380km and 560km, respectively. Given this limitation, I proceeded with the knowledge that I was examining long-range north-south dispersal only.

2.4 Statistical Analysis

I converted all feather deuterium values into “non-outlier” and “outlier” for Savannah Sparrow and Sprague’s Pipit by determining how much the P1 feather δD value differed from the expected local Last Mountain Lake feather δD value of -113‰ . A bird was classified as an outlier or non-outlier based on the two different ranges of variation ($\pm 6\text{‰}$ and $\pm 10\text{‰}$). Therefore, non-outlier birds had feather δD values between -107‰ and -119‰ or -103‰ and -123‰ . SPSS version 14 (SPSS 2005) was used for all statistical analysis.

I used logistic regression to determine whether breeding-site fidelity was correlated with breeding habitat and landscape surrounding the breeding habitat. Each bird was assigned a habitat classification (native or planted grass habitat) and a landscape classification (grass-dominated or crop-dominated landscape) based on the site where it was captured. Higher-quality sites were considered to be those that had sufficient resources for improved fitness. Although I did not directly measure fitness, I speculated on which habitats would have sufficient resources for improved fitness based on the life-history traits of my two study species. I speculated that native grass would be the highest-quality habitat because native prairie likely has a more diverse community of insects to feed on, more diverse vegetative community for nesting habitat and attracts more conspecifics for mating than planted grasslands. I used Akaike’s Information Criterion (adjusted for small sample size, AIC_c ; Burnham and Anderson 2002) to select among five candidate models. These models included habitat type and landscape type as main effects, as well as an additive model including both variables, an interaction model, and a null model.

The most parsimonious model was considered to be that with the lowest AIC_c value. All models with a ΔAIC_c value < 2 were considered to be competing models (Burnham and Anderson 2002). Akaike model weights were calculated to determine the weight of evidence that a given model was the best model of those I considered (Burnham and Anderson 2002).

I also used logistic regression to determine whether fidelity was correlated with landscape features at two different spatial scales (territory and landscape) because the first analysis was based on a subjective classification of landscape and habitat type. Sprague's Pipit territories in the study area have been estimated to be 2.5 ha (89 m radius around the capture point, R. Fisher, unpublished data) and Savannah Sparrow territories are approximately 1 ha (56 m radius around the capture point, Wheelwright and Rising 1993). I used a 1600 m radius around the capture point for both species, which was the scale at which abundance appeared to be best correlated with landscape features (Bergin et al. 2000, Bakker et al. 2002).

I considered six landscape variables that might influence a bird's fidelity to a breeding site; distance from capture point to nearest crop (DistCrop) and to the nearest road (DistRoad), as well as the percentage of native grass (TotNative), planted grass (TotTame), water (TotWater), and woody vegetative material (TotWood) within the buffer around the capture point. I analyzed the level of correlation among variables and did not include correlated variables ($p < 0.05$, based on correlation analysis in SPSS, alternatively $r > 0.25$) within the same model.

To differentiate among spatial scales in the model, each variable was also labeled with a number that corresponded to the meter radius around the capture point that was being quantified. For example, all variables quantified in a Savannah Sparrow territory were labeled with '56'.

The number of candidate models sets I considered varied between 39 and 60 models, depending on the species and which variables were correlated within those datasets. The

candidate model sets were determined using a stepwise procedure, starting with the null model and adding variables until the AIC_c value was no longer reduced. Main effect variables were run first, followed by all combinations of uncorrelated two-variable models (both additive and interaction models). Main effect variables were then added one by one to the two-variable model with the lowest AIC_c value. No three-variable model out-competed the top two-variable model for the lowest AIC_c value, so more complex models were not constructed. Although using a stepwise procedure in model selection has been criticized (Anderson and Burnham 2002), Anderson and Burnham (2002) do recognize that this approach might be useful in exploratory work, which is what I was doing.

2.5 Results

I captured 62 Sprague's Pipits and 111 Savannah Sparrows during the 2006 field season. Of these, 42 (68%) Sprague's Pipits and 59 (53%) Savannah Sparrows were outliers at the $\pm 6\%$ outlier classification and 32 (52%) Sprague's Pipits and 31 (28%) Savannah Sparrows were outliers at the $\pm 10\%$ outlier classification (Appendix B, Figure B.5 and Figure B.6).

2.5.1 Habitat – Landscape Categorical Analysis

I captured 65 individuals in crop-dominated landscapes, 108 in grass-dominated landscapes, 112 in native grass habitats and 61 in planted grass habitats (Table 2.1).

Landscape and habitat type had no effect on the fidelity of Sprague's Pipit or Savannah Sparrow. The null model was the most parsimonious model explaining variation in fidelity for both species (Appendix B, Table B.1, Table B.2, Table B.3, and Table B.4). Landscape and habitat type had no effect on the fidelity of either species.

Table 2.1. Number of outliers (and associated proportions) in each landscape and habitat type at Last Mountain Lake, SK, for both Sprague's Pipit and Savannah Sparrow at both the $\pm 10\text{‰}$ and $\pm 6\text{‰}$ outlier classifications.

		Savannah Sparrow			Sprague's Pipit		
		$\pm 10\text{‰}$	$\pm 6\text{‰}$	$n_{S\text{AVS}}$	$\pm 10\text{‰}$	$\pm 6\text{‰}$	$n_{S\text{PPI}}$
Habitat Type	<i>Native Grass</i>	19 (27%)	36 (51%)	71	21 (51%)	26 (63%)	41
	<i>Planted Grass</i>	12 (30%)	23 (58%)	40	11 (52%)	16 (76%)	21
Landscape Type	<i>Grass-dominated</i>	22 (31%)	38 (53%)	72	19 (53%)	25 (69%)	36
	<i>Crop-dominated</i>	9 (23%)	21 (54%)	39	13 (50%)	17 (65%)	26

2.5.2 Landscape Composition Analysis

Birds in all landscapes and habitat types were considered for the landscape composition analysis (62 Sprague's Pipits and 111 Savannah Sparrows). Distance to crop and roads ranged from 17 – 3471 m and 30 – 3031 m, respectively, for Sprague's Pipits and 0 – 3401 m and 18 – 3500 m, respectively, for Savannah Sparrows. Landscape composition variables ranged from 0 – 1.

The total percentage of water in the territory (TotWater89) was included in the most parsimonious model at both the $\pm 6\%$ ($w_i = 0.23$) and $\pm 10\%$ ($w_i = 0.09$) outlier classifications for Sprague's Pipit (Appendix B, Table B.5 and Table B.6). However, in both cases a suite of models had ΔAIC_c values < 2 , all with relatively low weights, suggesting high model uncertainty at both outlier classifications.

Large model uncertainty at the $\pm 10\%$ outlier classification, coupled with the null model being the most parsimonious ($w_i = 0.10$), suggests there was no effect of landscape composition on the fidelity of Savannah Sparrows (Appendix B, Table B.7). At the $\pm 6\%$ outlier classification, the model of DistR*TotWood56 ($w_i = 0.40$) had an effect on Savannah Sparrow fidelity such that Savannah Sparrows tend to be non-returning breeders further from roads with increasing percentage of total woody material (Appendix B, Table B.8 and Figure B.7).

2.6 Discussion

2.6.1 Habitat - Landscape Categorical Analysis

Sprague's Pipit breeding-site fidelity was not strongly correlated with habitat or the surrounding landscape. At both outlier classifications, the null model was the most parsimonious model, suggesting that other factors influence fidelity or that returning to a breeding area was a random occurrence. I expected native habitat and grass-dominated landscapes to have

individuals with higher fidelity because abundance is highest in native grasslands (Robbins and Dale 1999, Davis et al. 1999, Davis and Duncan 1999). More generally, Bakker et al. (2002) found that the amount of grassland in the landscape affected occupancy rates for grassland birds. Ribic and Sample (2001) suggest that landscape-level and habitat-level variables influence grassland bird densities, with the former being more influential (but see Koper and Shmiegelow 2006a).

As predicted, Savannah Sparrow fidelity was not strongly influenced by landscape and habitat type. Neither landscape nor habitat type affected Savannah Sparrow fidelity at either outlier classification, as the null model was the most parsimonious model in both cases. Therefore, my results suggest that neither landscape nor habitat type, as I defined them, affect the breeding fidelity of these species. I expected this to be the case, given that Savannah Sparrows are considered to be habitat generalists and are successful in a variety of habitats.

2.6.2 Landscape Composition Analysis

Landscape composition at both the landscape and territory spatial scales had little or no effect on the breeding-site fidelity of Sprague's Pipit. At both outlier classifications, the total amount of water in the territory was included in the most parsimonious model, although model selection uncertainty was high, with up to seven other competing models within 2 ΔAIC_c units of the best model. Furthermore, neither of these models explained much of the variance in the data ($R^2 = 0.15$ at the $\pm 6\%$ outlier classification and $R^2 = 0.09$ at the $\pm 10\%$ outlier classification).

An interaction between percentage of woody vegetation in a territory and the distance to the nearest road affected Savannah Sparrow fidelity at the $\pm 6\%$ outlier classification. However, despite this model being the most parsimonious and highly weighted of all models considered, it explained little variance in the data ($R^2 = 0.11$).

Savannah Sparrows tended to be outliers in areas with an increased total percentage of woody vegetation when further from roads. Areas with more woody vegetation typically have fewer Savannah Sparrows (Bakker et al. 2002). Low abundance may allow dispersing individuals to establish territories in those areas, which would explain my findings.

Savannah Sparrows tended to be outliers if their breeding territory was close to roads when there was no woody vegetation present. Koper and Schmiegelow (2006b) found the average number of upland songbird species per point count increased by 0.1 per km away from cropland and roads. This suggests that songbirds generally prefer to be further away from cropland and roads and may be less philopatric to sites that are close to cropland or roads. Brotons et al. (2005) suggest that an increased amount of similar habitat within the surroundings lead to an increase in species occurrence. Conversely, native or planted habitats that are close to cropland might experience a decrease in species occurrence, which would also suggest grassland songbirds prefer to be further away from cropland.

Sutter et al. (2000) evaluated the effect that roads and trails had on grassland songbird abundance in southern Saskatchewan. Sutter et al. (2000) found that Savannah Sparrows were more abundant along roads. They suggest that this is not surprising, given the species affinity for dense, grassy vegetation and use of roadside fences as elevated song perches. My findings suggest that Savannah Sparrows tend to be outliers near roads in the absence of woody vegetation. Perhaps individuals that have dispersed from elsewhere into the area find these roadsides attractive. Conversely, dispersing individuals may be forced to inhabit roadsides because they are able to secure territory near them more readily than in contiguous prairie. Finally, roadsides may be areas with low success and therefore experiencing high dispersal.

Although not found in this study, the total percentage of native grass within a territory has been identified as an important variable in Sprague's Pipit occurrence (Davis 2004, Wiens et al. 2007). However, native grass was not identified as an important variable in Savannah Sparrow occurrence (Davis 2004, Wiens et al. 2007). Furthermore, Ribic and Sample (2001) found that grassland songbird density decreased when the territory was nearer to woody material. However, this variable could not be included in my analysis given my methods of quantifying landscape attributes.

2.6.3 Limitations of This Study

Using stable hydrogen isotope analysis provided challenges in discerning a returning breeder from a non-returning breeder. I used two ranges of outlier classification to overcome potential bias in the extent of variation between feathers. Although $\pm 10\text{‰}$ accounts for a very extensive area (roughly 3 degrees of latitude; Wassenaar and Hobson 2006) and invariably results in some outlier birds being classified as non-outliers, the $\pm 6\text{‰}$ outlier classification is representative of the best case scenario and may not account for enough natural between-feather variation. However, Langin et al. (2007) found 80% of their known-origin birds had δD feather values within $\pm 6\text{‰}$ of the mean δD_f value, suggesting that $\pm 6\text{‰}$ may be an appropriate range of within-bird δD isotopic variation. I chose to have both conservative and liberal estimates of within-bird δD isotopic variation because I lacked known-origin birds and could not determine variance in feathers within this population.

Another limitation of this study was the coarse nature of the land cover data used to quantify landscape attributes, which prevented me from evaluating all possible scales at which fidelity may be influenced by landscape attributes. Although all quarter sections were ground truthed and the land cover data updated, pixel size was 30 m by 30 m, thus eliminating the option for

finer scale analysis. Landscape features at larger scales are typically positively correlated with smaller scale features. However, a small grouping of trees, which may not be associated with a large (greater than 30 m by 30 m) bluff of trees, could potentially affect a bird's reproductive success or survival by providing a perch for predator birds (Preston and Beane 1993, England et al. 1997). An unsuccessful breeding attempt may affect a bird's fidelity to that location in subsequent years. Future studies should consider quantifying landscape features on site, rather than relying on the use of land cover map layers in geographic information system programs as was done in this study, to account for finer scale features.

2.7 Retrospective Thoughts

It is possible that my definition of grass-dominated (>60% grass) and crop-dominated (<40% grass) landscapes did not incorporate enough of a difference in the amount of grass to warrant a true biological difference. These cut off points were arbitrary and future work may consider having a larger difference in the amount of grass between grass-dominated and crop-dominated landscapes.

Furthermore, given the necessity of only including sites where I found birds (as each site is characterized by the δD_f of the individual captured there), I may have biased my results. Perhaps tame grass habitats where I located individuals were actually acting as high-quality habitats, despite not being native grass. Therefore, my definition of a high-quality habitat may need to be expanded to include other habitat types which may also provide the resources necessary for improved fitness.

Finally, it was previously assumed that Sprague's Pipit and Savannah Sparrow were philopatric as a result of general knowledge about songbird philopatry and limited band returns (Jones et al. 2007, S. Davis, unpublished data). However, I found there to be a very high

proportion of non-returning breeders (Table 2.1), despite having a very conservative estimate of what constitutes a non-returning breeder and the large distance corresponding to my definition of an outlier. Therefore, these species are likely not as philopatric as previously thought. Perhaps a lack of breeding-site philopatry is actually an evolutionary advantage in the grasslands due to the stochastic nature of the grasslands (Johnson and Grier 1988, Jones et al. 2007). A suitable breeding habitat in one year could very well be crop in the following year, so the benefits to breeding-site philopatry (e.g. maintaining a high-quality breeding area, prior knowledge of the resources, predators, competition and conspecifics, etc.) may not be as strong of a driver as they would be in a more static landscape.

2.8 Conclusion

Grasslands are a unique landscape and grassland songbirds are relatively understudied. Future work needs to address the effect landscape composition may have on grassland songbird breeding-site fidelity at a finer scale. Although previous grassland bird research has looked at landscape attributes in more detail (e.g. Ribic and Sample 2001, Bakker et al. 2002, Renfrew and Ribic 2002, Davis 2004, Winter et al. 2005), they have not related it to breeding-site fidelity. Stable hydrogen isotope analysis offers a unique opportunity to overcome the challenges of studying breeding-site fidelity in songbirds. Although it is a tool that is better suited to large-scale analysis, patterns of dispersal can still be examined and lend evidence to what may be involved with a grassland songbirds' decision to return. The true strength of this technique is that it does not require marked individuals and as isoscapes undergo greater refinement, the resolution of the technique will be improved. There is a critical need to better understand factors affecting grassland songbird breeding-site fidelity so the landscape attributes they deem important to improve their fitness can be managed for and population decline can be reduced.

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CHAPTER 3: ROLE OF GEOGRAPHICAL LOCATION ON BREEDING DISPERSAL OF GRASSLAND PASSERINES: A STABLE HYDROGEN ISOTOPE (δD) APPROACH

3.1 Abstract

Given that environmental factors often change in a clinal manner, central populations presumably experience the most favorable environmental conditions and this favorability decreases with distance from the centre. Therefore, geographically peripheral locations may occur in ecologically marginal or stressful conditions. I examined the differences in the proportion of non-returning breeders at two geographically distinct locations; one centrally located within the Sprague's Pipit breeding range (Last Mountain Lake area, SK, Canada) and one at the periphery (Bowdoin National Wildlife Refuge, MT, USA). Using stable hydrogen isotope analysis, I determined the fidelity of grassland songbirds to these two locations. As expected, the Bowdoin National Wildlife Refuge had a significantly higher dispersal rate of Sprague's Pipits than the Last Mountain Lake area. Savannah Sparrow dispersal rates did not differ between locations at the $\pm 6\%$ outlier classification. Although Last Mountain Lake area is centrally located within the breeding ranges of both species, the Bowdoin National Wildlife Refuge is only central within the Savannah Sparrow breeding range, while being peripheral within the Sprague's Pipit breeding range. These results support the hypothesis that geographical position within the breeding range can influence dispersal rates of grassland songbirds.

3.2 Introduction

3.2.1 Geographical Location and Dispersal

Geographic distribution of a species generally correlates with the geographic distribution of species' physical (e.g. temperature, moisture, soil type) and biotic (e.g. distribution of predators,

competitors, resources, vegetation communities) environments (Grinnell 1917). Given that environmental factors often change in a clinal manner (Endler 1977), in general, central populations presumably experience the most favorable environmental conditions and this favorability decreases with distance from the centre (Lawton 1993). Therefore, geographically peripheral locations likely occur in ecologically marginal or stressful conditions (Lesica and Allendorf 1995).

Birds disperse from breeding areas for a variety of reasons, most of which relate to threats associated with survival and reproduction (Greenburg and Harvey 1982). Factors typically driving dispersal include resource acquisition, avoidance of predators or other means of mortality, competition avoidance, and proximity to conspecifics (Fahrig 2007). Birds disperse to improve their resources, decrease mortality and competition and increase conspecific interactions. Consequently, birds will tend to disperse from marginal or stressful environments. Given that geographically peripheral locations tend to be located in marginal or stressful environments, dispersal from these areas should be higher than at more central regions of a species' range.

3.2.2 Rationale and Objectives

Dispersal may have profound evolutionary and ecological consequences for populations (McPeck and Holt 1992, Hastings 1993, Kawecki and Holt 2002, Lowe 2003). From an evolutionary perspective, dispersal determines the level of gene flow among populations and affects local adaptation, speciation and the evolution of life-history traits (Dieckmann et al. 1999). From an ecological perspective, dispersal influences the dynamics and persistence of populations (Kareiva and Wennergren 1995, Mills and Allendorf 1996, Dieckmann et al. 1999), distribution and abundance of species, and community structure (Dieckmann et al. 1999).

Grassland bird populations in North America are declining faster and more consistently than any other group of birds (Sauer et al. 2005, Downes and Collins 2007). Despite this rapid decline, grassland bird populations are relatively understudied and little is known about the factors driving breeding-site philopatry and dispersal. Understanding factors influencing dispersal at different parts of a species' range would contribute to the general knowledge of these birds' life history, as well as allow managers to direct conservation efforts more effectively.

I used stable hydrogen isotope (δD) analysis of flight feathers to assess differences in dispersal rates of Sprague's Pipit (*Anthus spragueii*) and Savannah Sparrow (*Passerculus sandwichensis*) between the Last Mountain Lake National Wildlife Area and surrounding area (hereafter LML) and the Bowdoin National Wildlife Refuge (BNWR). These locations represented central and peripheral positions, respectively, within the Sprague's Pipit breeding range. In contrast, the Savannah Sparrow has a much larger breeding range, to which both locations were geographically central. By comparing dispersal rates of these two species, I determined if geographical location within the breeding range influenced dispersal.

I hypothesized that geographically peripheral locations would experience higher dispersal rates. I predicted there would be a larger proportion of non-returning Sprague's Pipit breeders at BNWR, given that this location is at the southern edge of their breeding range. I expected the proportion of non-returning Savannah Sparrow breeders would be similar between locations, as both are geographically central within the breeding range.

3.3 Methods and Study Design

3.3.1 Study Site

Feathers were collected at LML, Saskatchewan, Canada (51° 20' N, 105° 15' W) from May 1st, 2004 to July 31st, 2006 (Appendix D, Figure D.1). The landscape is a mosaic of native and

planted grassland and cropland. The surrounding area is primarily used for agricultural activities, such as annual cropping, haying and ranching (Appendix B, Figure B.1).

Feathers from Sprague's Pipits and Savannah Sparrows were also collected at BNWR in Montana, USA (48°24'N, 107°39'W) between May 1st, 2001 and July 31st, 2006 (Appendix D, Figure D.1). The BNWR is located in Phillips County and was established in 1936 as a migratory bird refuge (US Fish & Wildlife Service 2008). The BNWR encompasses 63 km² and is located in the short and mixed grass prairie region of north-central Montana (US Fish & Wildlife Service 2008). Comprised of saline and freshwater wetlands, native prairie, planted dense nesting cover and shrubs, the BNWR includes 27 km² of native mixed-grass prairie (US Fish and Wildlife Service 2008).

3.3.2 Study Species

Sprague's Pipit is a threatened ground-nesting passerine that is endemic to the Northern Mixed-grass Prairie (Mengel 1970). Sprague's Pipit breeds from southern and central Alberta, to west-central and southern Manitoba, and south to central Montana, northern South Dakota and northwestern Minnesota (Appendix B, Figure B.2). Its wintering range consists of the southern United States and the northern two-thirds of Mexico (Robbins and Dale 1999). Although still relatively common in areas with suitable habitat, populations in Alberta and Saskatchewan have declined by 6.0% and 4.9% per year, respectively, since 1968 (Downes and Collins 2007).

Numerous studies have suggested that Sprague's Pipit is strongly associated with native grasslands (Prescott and Davis 2000), preferring well-drained areas in open grassland (Robbins and Dale 1999) with moderate height and density and few shrubs or trees (Sutter et al. 2000, Grant et al. 2004). Furthermore, it is an area-sensitive species and is most abundant on larger tracts of contiguous prairie (Davis 2004, Davis et al. 1999). Sprague's Pipit is highly sensitive to

anthropogenic changes in its breeding habitat and is a good indicator of grassland quality in the Canadian prairies (Prescott and Davis 2000).

The Savannah Sparrow is a common ground nesting passerine that breeds throughout Canada and the United States, ranging from Alaska and the Canadian territories to coastal southern California, northern New Mexico and the Great Lakes region (Appendix B, Figure B.3). They winter in the southern United States, Guatemala, Belize, throughout most of Mexico, and on various islands in the Caribbean (Wheelwright and Rising 1993).

In contrast to Sprague's Pipit, the Savannah Sparrow is commonly found in both native and non-native grassland habitats (Davis and Duncan 1999, McMaster and Davis 2001) and is considered a grassland habitat generalist, being found in grassy meadows, cultivated fields, lightly grazed pastures, roadsides, coastal grasslands, sedge bogs, edges of salt marshes and tundra (Wheelwright and Rising 1993). Savannah Sparrows avoid trees (Grant et al. 2004, Wheelwright and Rising 1993), but are not sensitive to habitat patch-size (Johnson and Igl 2001, Davis 2004).

3.3.3 Avian Sampling

Individuals were captured at LML using playback recordings, a decoy and two 6 m mist nets. Mist nets were set up in a V-formation with a focal-species specific decoy placed where the mist nets meet. A digital caller (Western Rivers Predation MP3 game caller) was placed next to the decoy and a focal-species specific territorial male call broadcasted. At the BNWR, a Sony TC-D5Pro II or Marantz PDM 430 cassette recorder amplified by an AMpliVox s805 Multimedia Amplifier, connected into two tweeters by 30-50 m of 16-guage speaker cord, was used to broadcast the focal-species specific territorial male call and speakers were placed on either side of a 12 m mist net. Painted wooden decoys were placed at the net as lures beginning in 2003.

Once captured, birds were marked, sexed, aged, morphological measurements were taken, and feather samples collected (see below). All birds were marked with a USGS Service aluminum band. Birds were sexed according to presence or absence of brood patch and cloacal protuberance. Morphological measurements were taken according to Monitoring Avian Productivity and Survivorship (MAPS) banding station protocol (DeSante et al. 2008).

The first primary (P1) of the wing and fourth rectrix (R4) of the tail were removed by LML researchers, as these feathers are replaced on the previous year's breeding grounds (Pyle 1997). The BNWR researchers typically sampled R4, although occasionally another rectrix (excluding the inner rectrix, R1, and the outer rectrix, R6) was sampled opportunistically. These feathers (R2 thru R5) are also replaced on the previous year's breeding grounds (Pyle 1997). Feathers were usually pulled, rather than clipped, to initiate regrowth and reduce the impact on flight. Each feather was placed in a labeled paper envelope.

3.3.4 Laboratory Analysis

Feather samples were cleaned of surface oils in 2:1 chloroform:methanol solution overnight, drained and air dried under a fumehood. Feather samples were then cut and $0.35 \text{ mg} \pm 0.02 \text{ mg}$ was weighed into 4.0 mm x 3.2 mm silver capsules for online hydrogen isotope analysis by continuous-flow isotope-ratio mass spectrometry (CFIRMS). Stable hydrogen isotope (δD) analytical measurements followed the "comparative equilibration" technique described by Wassenaar and Hobson (2003). Briefly, the process involves the measurement of unknowns with several replicates of three different keratin standards whose nonexchangeable δD values are known and which span the range of expected feather values. This provided a way of correcting for uncontrolled isotopic exchange between samples and ambient water vapor (Wassenaar and

Hobson 2000, Hobson et al. 2004) so that the values reported are equivalent to nonexchangeable feather hydrogen.

Isotopic values were expressed in delta notation in parts per thousand (‰) as the non-exchangeable hydrogen portion of samples normalized on the Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale. Feather samples were analyzed at the stable isotope facility of the National Hydrology Research Centre in Saskatoon, Canada.

3.3.5 Local Deuterium Values and Outlier Definition

To determine mean growing-season precipitation δD values for the LML area and the BNWR I used interpolated GIS-based models of stable hydrogen isotope ratios in North America derived from growing-season precipitation (See Appendix C). This approach involves using a version of the Bowen et al. (2005) isoscape corrected for annual variation in precipitation to determine the expected weighted average mean growing-season precipitation deuterium value (δD_{p-gs}) for a specific location (i.e. LML and BNWR) in a specific year. These δD_{p-gs} values are then converted to a feather deuterium value (δD_f) by regressing δD_{p-gs} on δD_f (Appendix C, Equation C.2).

I determined ranges of within-feather δD isotopic variation to categorize individual birds as returning (herein non-outlier birds) or non-returning birds (herein outlier birds) to the breeding grounds. Two ranges of variation about the calculated expected mean local feather value were used. I chose $\pm 6\text{‰}$ based on Wassenaar and Hobson (2006) who found that within-feather δD isotopic variance for captive birds was as low as $\pm 3\text{‰}$ for vane material and suggest a more realistic variance to expect is on the order of $\pm 6\text{‰}$. Langin et al. (2007) found $\pm 6\text{‰}$ to be an appropriate variance in American redstarts (*Setophaga ruticilla*). An outlier classification of

$\pm 10\text{‰}$ outside of the expected local feather mean was also chosen *a priori* to discriminate between local birds and outliers. This value was appropriate after reviewing the range of between-feather variation within individual birds captured at LML in 2004 thru 2006 (Appendix D, Figure D.2). I compared δD_f values from P1 and R4 taken from each individual, as both feathers should have been grown on the breeding grounds and therefore should have the same δD_f value. Feathers with δD_f values suggesting adventitious replacement by having a δD_f value outside the breeding range were not considered. P1 and R4 were significantly correlated ($r = .36, p = 0.04, n = 34$ and $r = .60, p = 0.00, n = 30$ for Savannah Sparrow and Sprague's Pipit, respectively) and 72% of the birds had P1 and R4 signatures that were within 10‰ of one another.

3.4 Statistical Analysis

3.4.1 General Information

I converted all δD_f values into non-outliers and outliers for Savannah Sparrow and Sprague's Pipit by determining how much the bird's δD_f value differed from the expected year-specific local δD_f values (Table 3.1). The bird was classified as an outlier or non-outlier bird, based on the two different ranges of variation ($\pm 6\text{‰}$ and $\pm 10\text{‰}$).

3.4.2 Feather Type Comparison

In some cases only R4 was pulled and if R4 did not accurately represent the individual's prior breeding ground (which is most reliably detected in P1, Pérez 2006), then these individuals could not be included in analysis. I did a correlation analysis (SPSS Inc. 2005) to determine if the P1 and R4 feather deuterium value from an individual were correlated.

Table 3.1. Year-specific δD_{p-gs} and δD_f values for Last Mountain Lake, SK and Bowdoin National Wildlife Refuge, MT.

Site	Year	Year-specific δD_{p-gs}	Year-specific δD_f
Last Mountain Lake, SK	2003	-107	-120
	2004	-101	-115
	2005	-99	-113
Bowdoin National Wildlife Refuge, MT	2000	-96	-110
	2001	-93	-108
	2002	-93	-108
	2003	-99	-114
	2004	-95	-109
	2005	-90	-105

3.4.3 National Wildlife Area vs. Non-National Wildlife Area Comparison

Individuals at LML were captured both within and outside the LML National Wildlife Area. I determined if the proportion of outlier birds within and outside the LML National Wildlife Area differed by conducting a z-test of proportions (Zar 1999) on the proportion of outliers in each area. All data were grouped by species and outlier classification.

3.4.4 LML vs BNWR Comparison

I determined to what degree the proportion of outliers at LML differed from the proportion of outliers at the BNWR using a z-test of proportions (Zar 1999, $z_{critical} = 2.25$ after applying a Bonferonni correction to account for comparison of data at two outlier classifications). All data were grouped by species and outlier classification. Individuals captured in all years were amalgamated at both locations because too few individuals were captured in some years to do year-specific comparisons.

3.5 Results

During the 2004 thru 2006 field seasons, 151 Savannah Sparrows and 186 Sprague's Pipits were captured at LML. Between 2001 and 2006, 15 Savannah Sparrows and 27 Sprague's Pipits were captured at the BNWR.

3.5.1 Feather Type Comparison

A total of 34 Savannah Sparrows and 30 Sprague's Pipits were used to compare between P1 and R4 feather deuterium values of each individual (Appendix D, Figure D.2). Within Savannah Sparrows, P1 and R4 feathers were significantly correlated ($r = .36, p = 0.04, n = 34$). Sprague's Pipit P1 and R4 feathers were also significantly correlated ($r = .60, p = 0.00, n = 30$). P1 was

used to represent an individual's δD_f value preferentially, but in the cases where no P1 was available, R4 was converted to P1 using the regression equation calculated in the above correlation analysis to represent the individual.

3.5.2 National Wildlife Area Comparisons

There was no difference in the proportion of outliers caught on the National Wildlife Area compared to those outside the National Wildlife Area at LML (Appendix D, Table D.1). Therefore all individuals (both those captured on and outside of the LML National Wildlife Area) were included in the final proportion of outliers at LML.

3.5.3 LML vs BNWR Comparison

I determined the proportions of outliers for each species at each classification level so I could evaluate differences between proportions of outliers at these two locations (Table 3.3). The proportions of outliers of Sprague's Pipits differed significantly between LML and the BNWR at the $\pm 10\text{‰}$ outlier classification (Table 3.3). BNWR had a significantly ($p = 0.04$) higher proportion of outliers than LML. The comparison between the proportion of Sprague's Pipit outliers between LML and BNWR at the $\pm 6\text{‰}$ outlier classification showed a similar trend towards significance, as the z-value neared the critical z-value (2.25).

The proportion of Savannah Sparrow outliers did not differ significantly between locations at the $\pm 6\text{‰}$ outlier classification. However, at the $\pm 10\text{‰}$ outlier classification, BNWR had a significantly larger proportion of outliers than LML.

According to the distribution of observed δD_f values, Sprague's Pipits tend to be dispersing from the south and Savannah Sparrows tend to be dispersing from the north at LML (e.g.

Appendix D, Figure D.3). Although BNWR had much fewer individuals, similar trends were evident.

Furthermore, large differences in the proportion of outliers between the $\pm 6\%$ and $\pm 10\%$ outlier classifications (Table 3.3) were present at LML. These differences were not as pronounced at BNWR.

3.6 Discussion

Dispersal rates of Sprague's Pipits were higher at BNWR than at LML lending some evidence that location within the breeding range affects dispersal rates. Dispersal rates of Savannah Sparrows did not differ (at the $\pm 6\%$ outlier classification) between these two locations, which are both central to the Savannah Sparrow breeding range, lending further support to the hypothesis that location within the breeding range affects dispersal rate.

However, BNWR had a significantly large proportion of outlier Savannah Sparrows at the $\pm 10\%$ outlier classification. This result was unexpected, given the generalist nature of Savannah Sparrows. These results do not consistently support my hypothesis that peripheral locations have higher dispersal rates. One of the limitations of this study is that I was only able to examine dispersal rates at two sites, rather than having replicates of sites at both the center and periphery of the breeding range. Therefore, I may have detected site differences between BNWR and LML, rather than differences between the periphery and the center of the breeding range. Further work is needed to determine if the differences between these two sites are truly related to their geographic position within the breeding range or if the differences are site-specific.

Table 3.3. Proportion of outlier birds at each outlier classification level and the z-test of proportions of outlier birds captured at Last Mountain Lake (LML), SK, Canada in comparison to those captured at the Bowdoin National Wildlife Refuge (BNWR), MT, USA between May 1st, 2001 and July 31st, 2006. The critical z-value is 2.25 (after applying a Bonferonni correction for comparison of data at two outlier classifications). Analysis incorporated 151 and 15 Savannah Sparrows, as well as 186 and 27 Sprague's Pipits, at LML and BNWR, respectively.

Species (Outlier Classification)	Proportion of Outliers at LML	Proportion of Outliers at BNWR	z-value	p-value
Savannah Sparrows ($\pm 10\%$)	0.31	0.60	-2.31	0.04
Savannah Sparrows ($\pm 6\%$)	0.54	0.67	-0.97	0.66
Sprague's Pipits ($\pm 10\%$)	0.54	0.78	-2.31	0.04
Sprague's Pipits ($\pm 6\%$)	0.66	0.85	-2.00	0.09

The structure of the observed δD_f values at both LML and BNWR indicated that Sprague's Pipits disperse from the south and Savannah Sparrows disperse from the north. These results are consistent with Sprague's Pipits having a greater proportion of dispersers at BNWR. Furthermore, the Savannah Sparrow breeding range extends farther to the north than the Sprague's Pipit breeding range (Appendix B, Figure B.2 and Figure B.3).

The larger differences in the proportion of outliers between the $\pm 6\%$ and $\pm 10\%$ outlier classifications at LML suggest that outliers are dispersing from closer at LML than they are at BNWR. Isoscapes depicting the probability an individual originated from an area, also known as probability surfaces, confirm that outlier Sprague's Pipits at LML are dispersing from closer than those at BNWR (Figure 3.2).

In the case of LML at the $\pm 6\%$ outlier classification, the highest proportion of outliers seems to be originating near LML. This might be an artifact of the outlier classifications I used. The $\pm 6\%$ outlier classification may be too narrow causing local birds to be misclassified as outliers. This result contradicts the literature (Wassenaar and Hobson 2006, Langin et al. 2007), which suggests $\pm 6\%$ is an appropriate δD_f variation within a wild population. However, this probability surface is not based on a year-specific corrected Bowen et al. (2005) isoscape, but rather the original Bowen et al. (2005) isoscape, which could be the cause of some of the non-returning birds' appearance to have originated at LML.

The dispersal rates for both LML and BNWR are generally higher than those published in the literature. Using a different approach to classifying an outlier based on its δD_f value, Hobson et al. (2004) found the proportion of non-returning ASY Ovenbirds (*Seiurus aurocapillus*) to be between 0.00 and 0.15. The proportion of non-returning ASY American Redstarts (*Setophaga ruticilla*) was between 0.00 and 0.12. However, Scheiman et al. (2007) also found

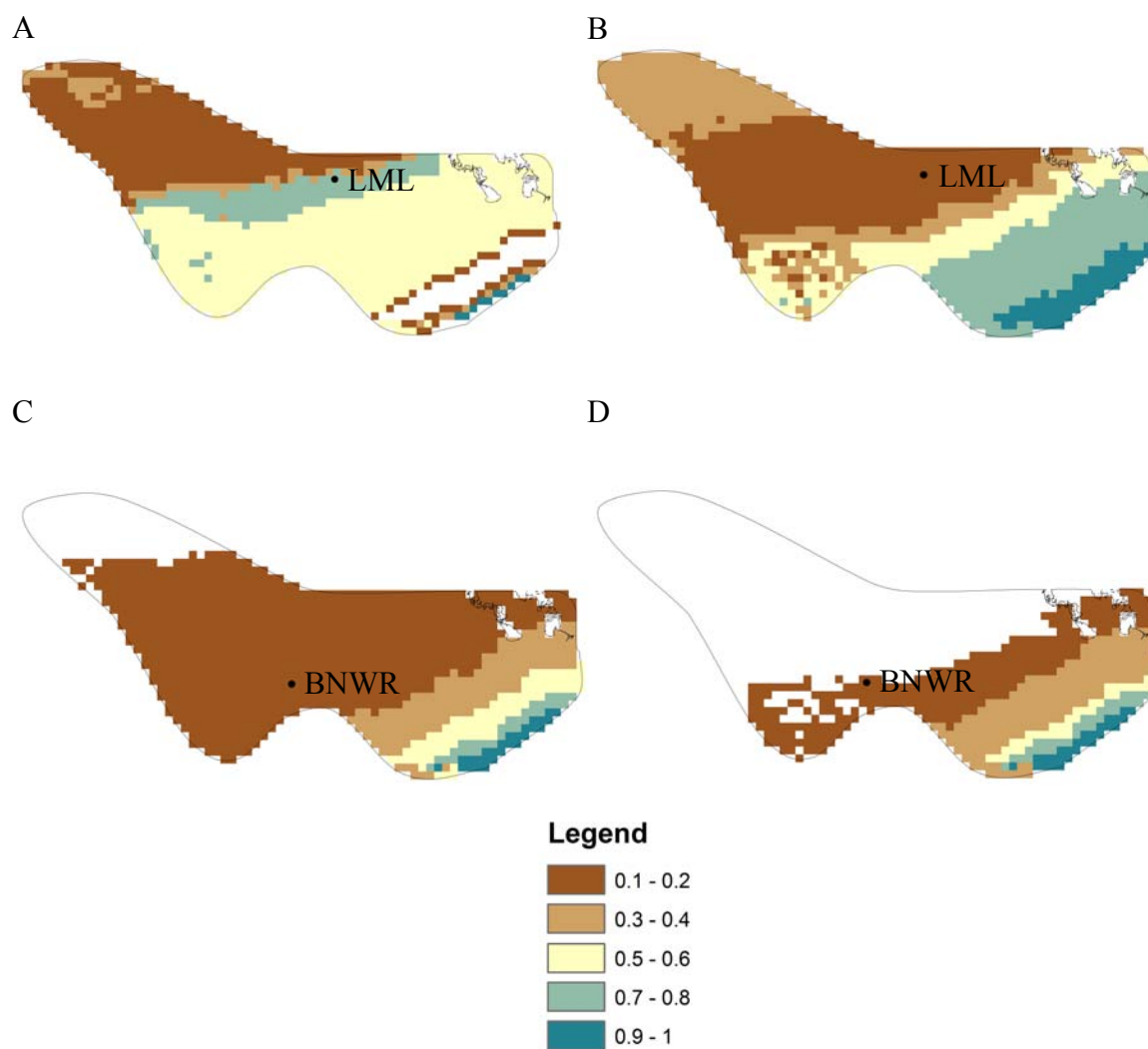


Figure 3.2. Relative probability that an outlier Sprague's Pipit originated from an area within the breeding range. A) Outliers ($\pm 6\%$) captured at LML B) Outliers ($\pm 10\%$) captured at LML C) Outliers ($\pm 6\%$) captured at BNWR D) Outliers ($\pm 10\%$) captured at BNWR. Probability surface was created using methods described in Royle and Rubenstein (2004).

relatively high adult dispersal rates in Bobolinks (*Dolichonyx oryzivorus*), but do not quantify the inter-annual dispersal. Perhaps a lack of breeding-site philopatry is actually an evolutionary advantage in the grasslands due to the stochastic nature of the grasslands (Johnson and Grier 1988, Jones et al. 2007).

Although there are many possible hypotheses as to why BNWR is experiencing higher dispersal rates than LML, I did not have adequate data to investigate these possible hypotheses. Future studies should focus on identifying the causes for increased dispersal at BNWR.

3.7 Conclusion

Dispersal rates of Sprague's Pipit were higher at the periphery of the breeding range. Other grassland songbirds may exhibit similar differences in dispersal at central and peripheral locations within their breeding ranges. Future research should focus on determining whether differences in dispersal rates at the two sites can be consistently attributed to the position within the breeding range, rather than a site effect. If it turns out that there is indeed an effect of geographical location, it should then be determined which environmental factor(s) of geographically peripheral locations are causing dispersal or which factor(s) of central locations make them attractive to grassland songbirds. Stable hydrogen isotope analysis would be a useful tool in this endeavor because it allows us to detect large-scale dispersal. Ultimately, understanding these mechanisms would allow managers to more effectively preserve areas that would be beneficial to grassland songbirds.

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CHAPTER 4: SUMMARY AND SYNTHESIS

Grassland bird populations are declining at an alarming rate (Sauer et al. 2005, Downes and Collins 2007), likely as a result of loss and degradation of grassland habitat (Samson and Knopf 1994, Riemer et al. 1997, Askins et al. 2007). For conservation to be effective, it is essential that we ascertain how birds perceive grassland habitats at various spatial scales and what impact this has on the likelihood that they settle or return to these areas (Bakker et al. 2002). Breeding- and natal-site philopatry in songbirds has been relatively understudied, in part due to the difficulty in tracking individuals using conventional mark-recapture methods. Stable hydrogen isotope (δD) analyses offer an alternative to the conventional mark-recapture techniques. This is the first study to use δD analysis of feathers to assess fidelity of migrant grassland songbirds to differing landscapes and habitats.

Landscape and habitat composition may influence breeding-site fidelity of grassland songbirds (Bollinger and Gavin 1989, Korpimäki 1993, Stanback and Rockwell 2003). High-quality sites are likely to have a higher percentage of return breeders than low-quality sites because they may have more or higher-quality resources birds need for successful reproduction. Successful birds are more likely to return than unsuccessful birds (see Bollinger and Gavin 1989). In Chapter 2, I used δD analysis to determine the fidelity of grassland songbirds to two habitat and two landscape types. Habitat type was defined at the quarter section level and landscape composition included a one mile buffer around the quarter section. I hypothesized that there would be a larger proportion of returning grassland birds on higher quality sites. For Sprague's Pipit (*Anthus spragueii*), a grassland habitat specialist, I expected a higher proportion of returning breeders to native grass habitat in grass-dominated landscapes. Given that Savannah Sparrow (*Passerculus sandwichensis*) is a habitat generalist, I expected no difference in return

rate to either habitat or landscape. However, the proportion of non-returning breeders did not significantly differ on either landscape or habitat for either Sprague's Pipit or Savannah Sparrow.

I examined the affect landscape and habitat composition may have on breeding-site fidelity further by quantifying attributes (distance from capture point to nearest crop and to the nearest road, as well as the percentage of native grass, planted grass, water, and woody vegetative material) of the landscape and territory of each individual to determine if specific attributes of the landscape or territory influenced the return rate to a breeding area. However, neither species exhibited a strong relationship with any of the landscape or territory characteristics considered. This finding is surprising because prior density and abundance studies have suggested that both landscape and habitat characteristics influence settlement patterns (Davis et al. 1999, Ribic and Sample 2001, Bakker et al. 2002). Abundance may reflect return rates, suggesting landscape and territory composition may have an impact on return rates. In this study, the definition of landscape characteristics was quite broad (i.e. native grass, planted grass, wetland). Perhaps individuals based their decision to return on more precise landscape characteristics (i.e. native mid-grass prairie, alfalfa or temporary wetlands). Future studies should consider defining landscape characteristics more precisely than was done here. Digitized air photos could be used, rather than the South Digital Land Cover Landsat imagery that was used in this study, to gain more detailed habitat information. This method, combined with detailed ground surveys, would greatly improve the resolution and would allow landscape characteristics to be more precisely defined. For example, the native prairie classification could be separated further by vegetation height and density, as these may play a role in nest selection and success of ground nesting passerines (Sutter 1997, Dieni and Jones 2003, Davis 2005).

One other consideration that arose from the use of stable isotopes in Chapter 2 was that of knowing the exact molt strategy to ensure appropriate feathers were being sampled. Future studies would benefit from knowing the exact molt strategy of the species they are interested in. In this study, molt strategy was derived from Pyle (1997) and personal observations (S. Davis) in the field and was supported by the distribution of observed feather deuterium (δD_f) values. However, for many studies, personal observations of molt strategy may not be available and it would be time and cost-effective to know, prior to sampling, which feather is the most appropriate feather to analyze. Stable hydrogen isotope analysis would be an effective tool to assess molt strategy and work is already in progress to address the molt strategy of Sprague's Pipits (Davis et al., unpublished data) further.

In Chapter 3, I addressed the potential differences in dispersal rates at central and peripheral locations within the Sprague's Pipit breeding range. Given that environmental factors often change in a clinal manner (Endler 1977), central populations presumably experience the most favorable environmental conditions and this favorability decreases with distance from the center (Lawton 1993). Therefore, geographically peripheral locations likely occur in ecologically more marginal or stressful conditions (Lesica and Allendorf 1995).

I examined differences in dispersal rates at two geographically distinct locations; one centrally located in the Sprague's Pipit breeding range (Last Mountain Lake area, SK, Canada) and one at a more peripheral location (Bowdoin National Wildlife Refuge, MT, USA). Using stable hydrogen isotope analysis, I determined the fidelity of grassland songbirds to these two locations. As expected, the Bowdoin National Wildlife Refuge had a significantly larger dispersal rate of Sprague's Pipits than the Last Mountain Lake area at the liberal outlier classification, but there was only a trend in this direction at the conservative outlier

classification. Savannah Sparrow dispersal rates did not differ between locations at the conservative outlier classification, but had a significantly higher proportion of non-returning breeders at the Bowdoin National Wildlife Refuge at the liberal outlier classification. Although Last Mountain Lake area is centrally located within the breeding ranges of both species, the Bowdoin National Wildlife Refuge is only centrally located within the Savannah Sparrow breeding range. These results provide limited evidence that geographical position within the breeding range can influence dispersal rates, such that birds are more likely to be dispersing breeders at the periphery of the breeding range, but caution is recommended in interpretation.

Further work should be conducted to determine how these two sites differ among years. If Bowdoin National Wildlife Refuge consistently has a higher proportion of non-returning Sprague's Pipits, but not Savannah Sparrows, then one could further investigate the hypothesis that the periphery has greater dispersal than central regions of the breeding range. Commonly cited reasons for dispersal at the periphery include fewer or lower-quality resources (Fahrig 2007), increased competition (Maurer 1999, Husak and Linder 2004), fewer conspecifics (Muller et al. 1997, Ahlering et al. 2006, Nocera et al. 2006, Fahrig 2007) or an increased number of predators (Fahrig 2007). Knowing what causes dispersal at the periphery may lead to a better understanding of the factors affecting a grassland bird's choice to settle or return to a breeding area and would subsequently allow for more directed conservation efforts to ensue.

The local precipitation amount weighted average deuterium value (δD_p) during the growing-season at locations within grassland ecosystems differed from that described by the stable hydrogen isotope ratio basemaps, illustrated in Hobson and Wassenaar (1997), Meehan et al. (2004) and Bowen et al. (2005). In Appendix C, I described how the Bowen et al. (2005) isoscape can be improved by accounting for isotopic variance explained by geographic location

and year-to-year variation in precipitation amount within the Great Plains. By accounting for longitude and the coefficient of variation within precipitation in a single year at a specific location, I determined a year- and site-specific best estimate of δD_p . This method of determining local weighted growing-season δD_p is an improvement upon the Bowen et al. (2005) isoscape, as demonstrated by the comparison of known-source feathers and the estimated δD_f value for that location in the year of growth. Future research involving the assignment of individuals to origins based on their δD_f values should incorporate year-to-year variation by applying year-specific corrections of the Bowen et al. (2005) isoscape for improved assignment. This will require fairly complete or improved δD_p data as was used in Appendix C.

There is a critical need to better understand factors affecting grassland songbird breeding-site philopatry and dispersal. I have done some of the preliminary work and have improved our ability to address questions of grassland songbird breeding-site philopatry and dispersal, but much more work is needed. The current state of grassland songbirds is dire, but with appropriately directed research and conservation, we have the opportunity to prevent the situation from getting worse.

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APPENDIX A: BAIRD'S SPARROW ANALYSIS

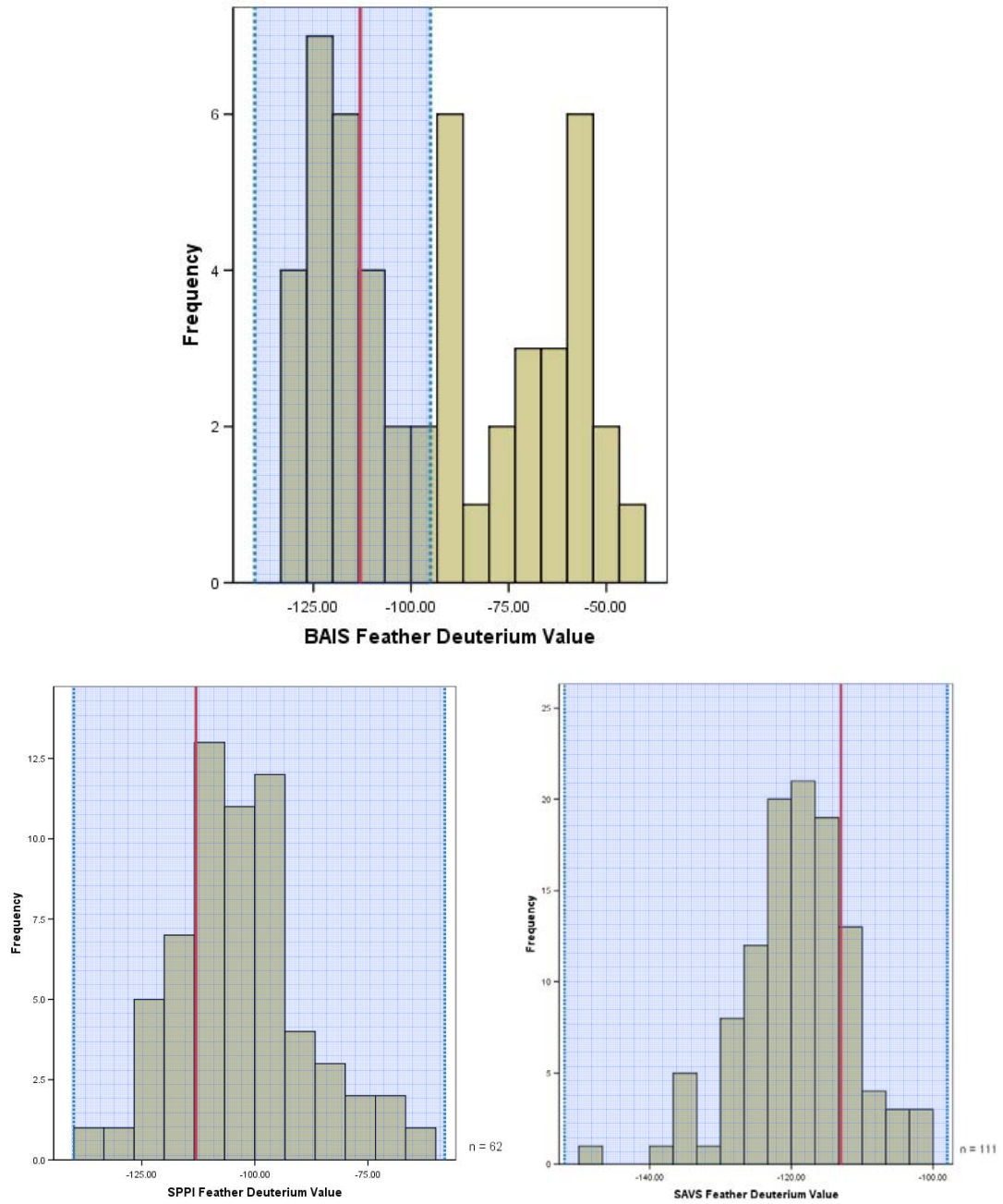


Figure A.1. Distribution of Baird's Sparrow (BAIS) P1 δD_f values ($n = 49$) at Last Mountain Lake, SK, captured in 2006. For comparison, Sprague's Pipit (SPPI) and Savannah Sparrow (SAVS) distributions of observed P1 δD_f values at Last Mountain Lake are included. The blue transparent areas outline the breeding range of each species.

APPENDIX B: SUPPLEMENTAL FIGURES AND TABLES FROM CHAPTER 2

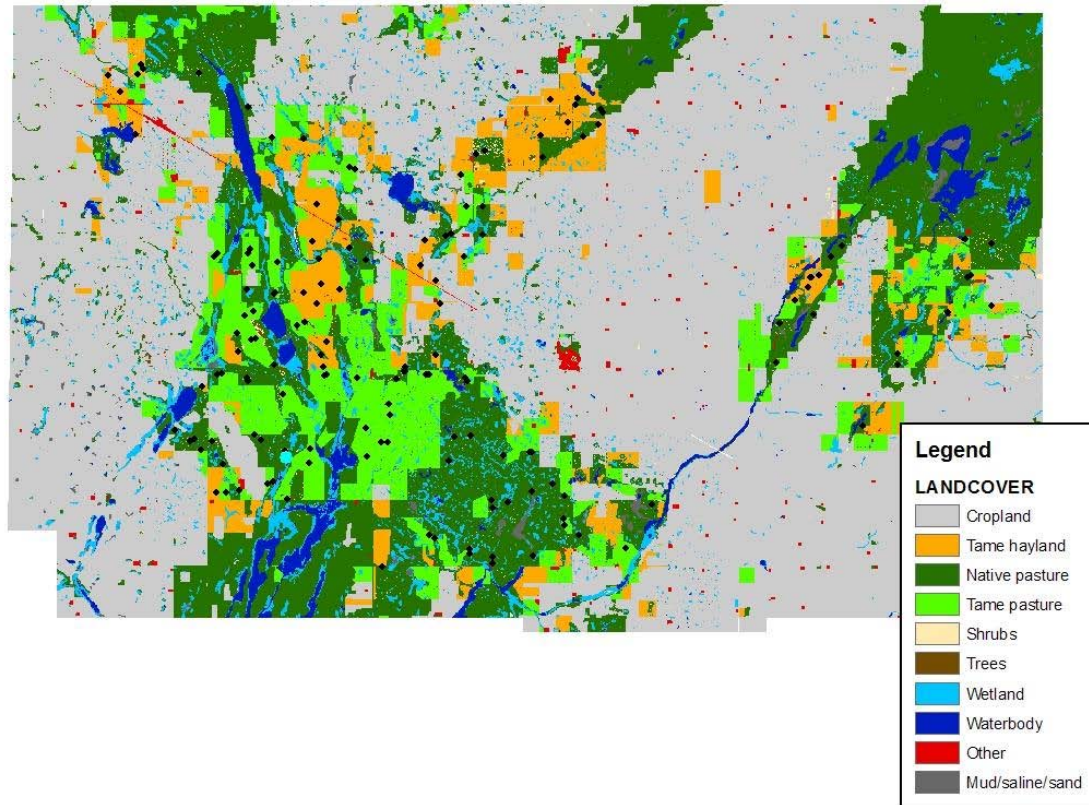


Figure B.1. Land cover map of the north end of Last Mountain Lake, SK, Canada in 2006. Capture locations of all individuals are denoted by black circles.



Figure B.2. Distribution of the Sprague's Pipit across North America (Robbins and Dale 1999).



Figure B.3. Distribution of the Savannah Sparrow across North America (Wheelwright and Rising 1993).

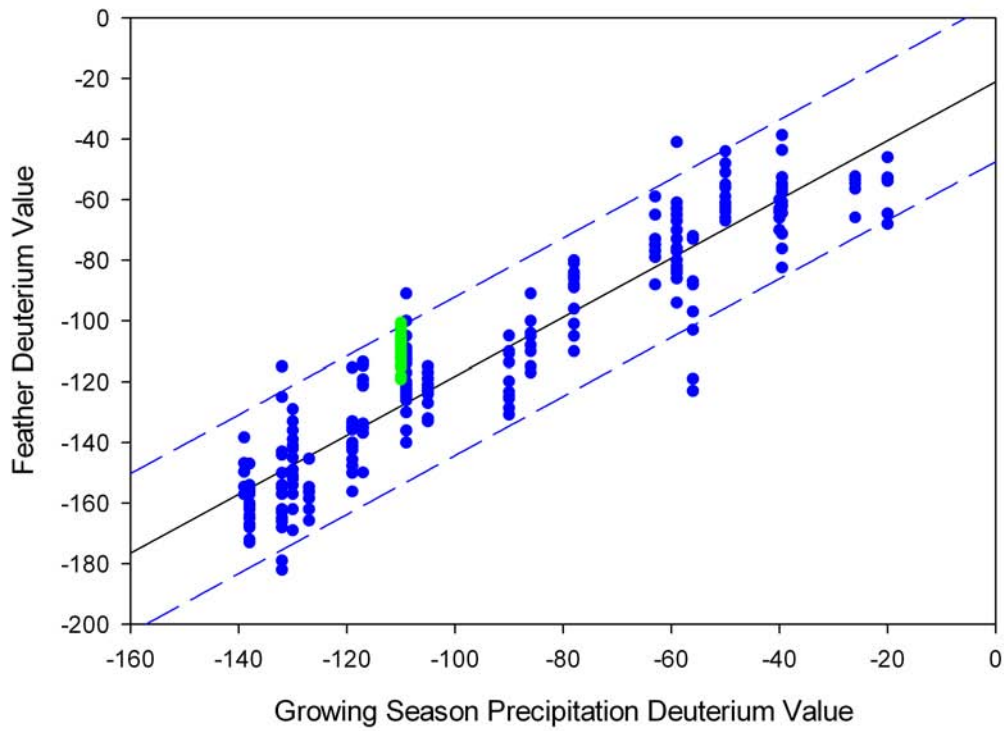


Figure B.4. Relationship between δD values in feathers versus that predicted in δD values in growing-season precipitation across North America. Blue circles indicate the Clark et al. (2006) data and green circles indicate Sprague's Pipit data from Last Mountain Lake in 2006.

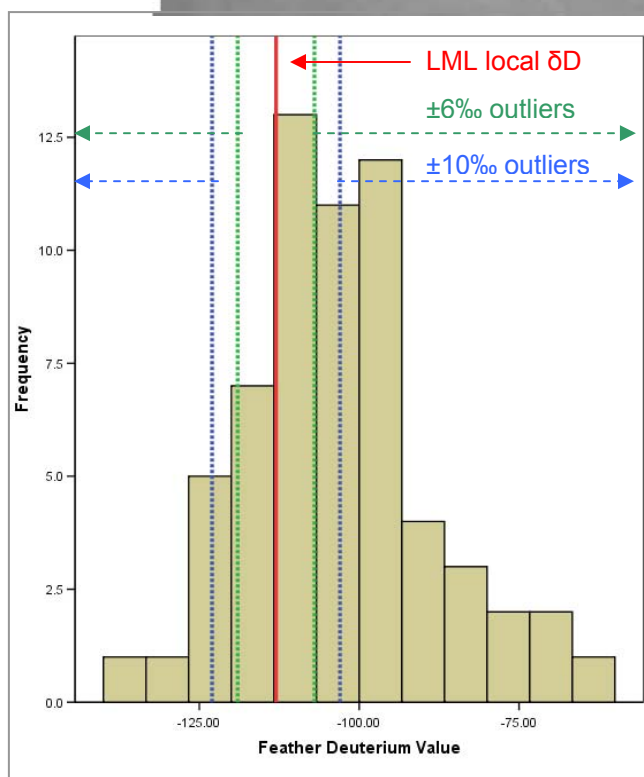
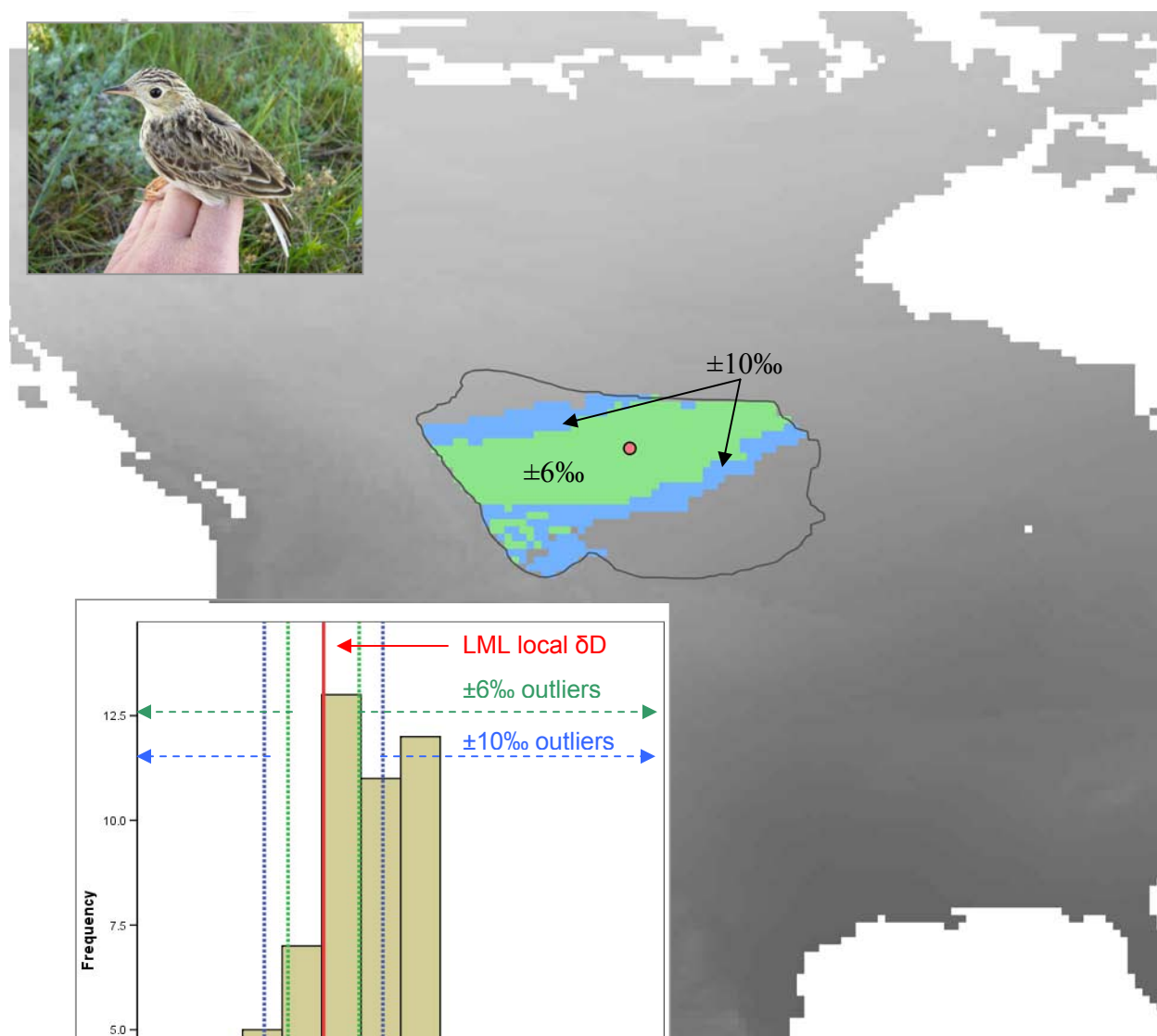


Figure B.5. Distribution of Sprague's Pipit P1 δD_f values at Last Mountain Lake, SK captured in 2006. Grey outline indicates the Sprague's Pipit breeding range.

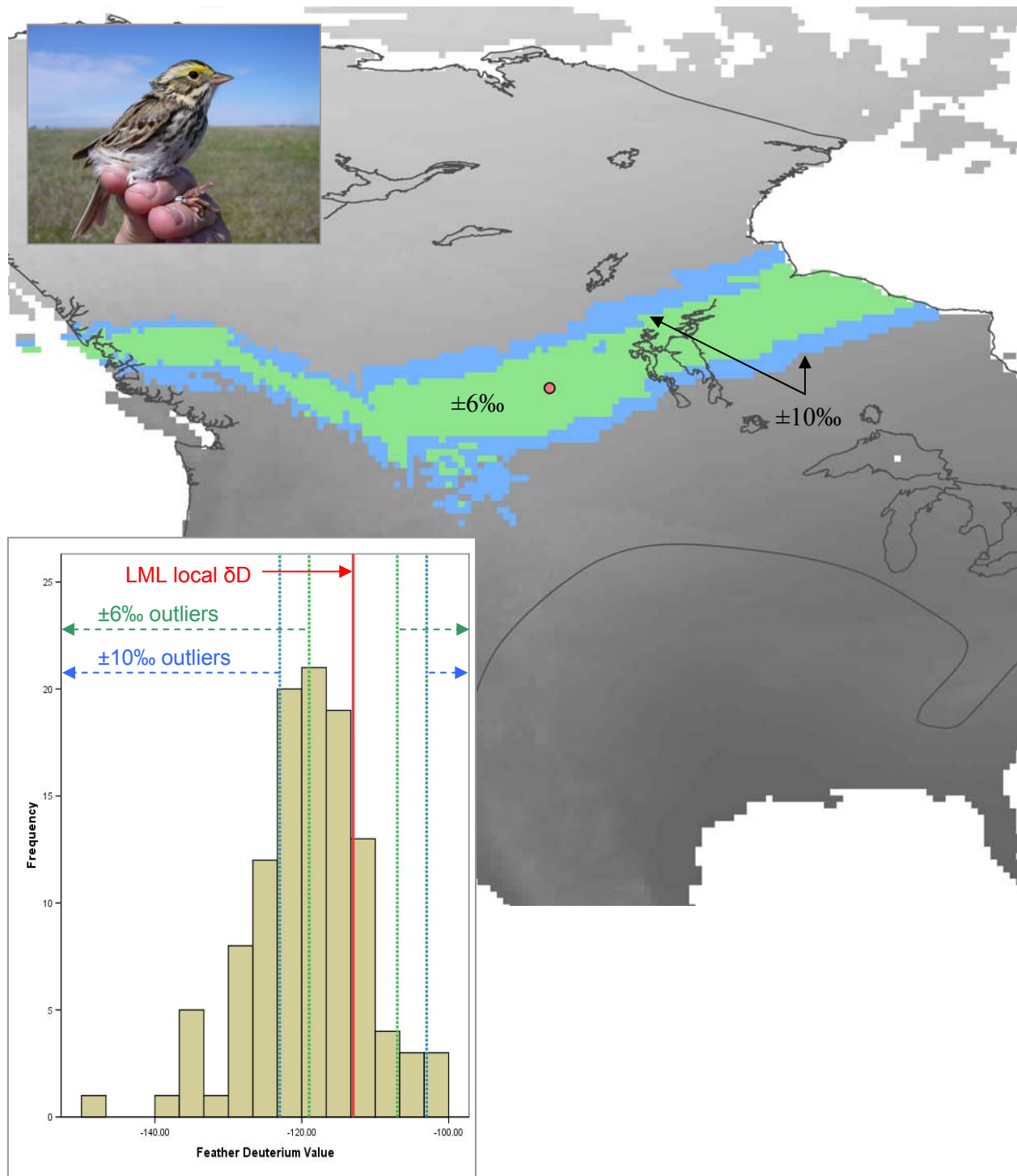


Figure B.6. Distribution of Savannah Sparrow P1 δD_f values at Last Mountain Lake, SK captured in 2006. Grey outline indicates the Savannah Sparrow breeding range. Individuals at Last Mountain Lake, SK, are unlikely to have originated from west of the Rocky Mountains.

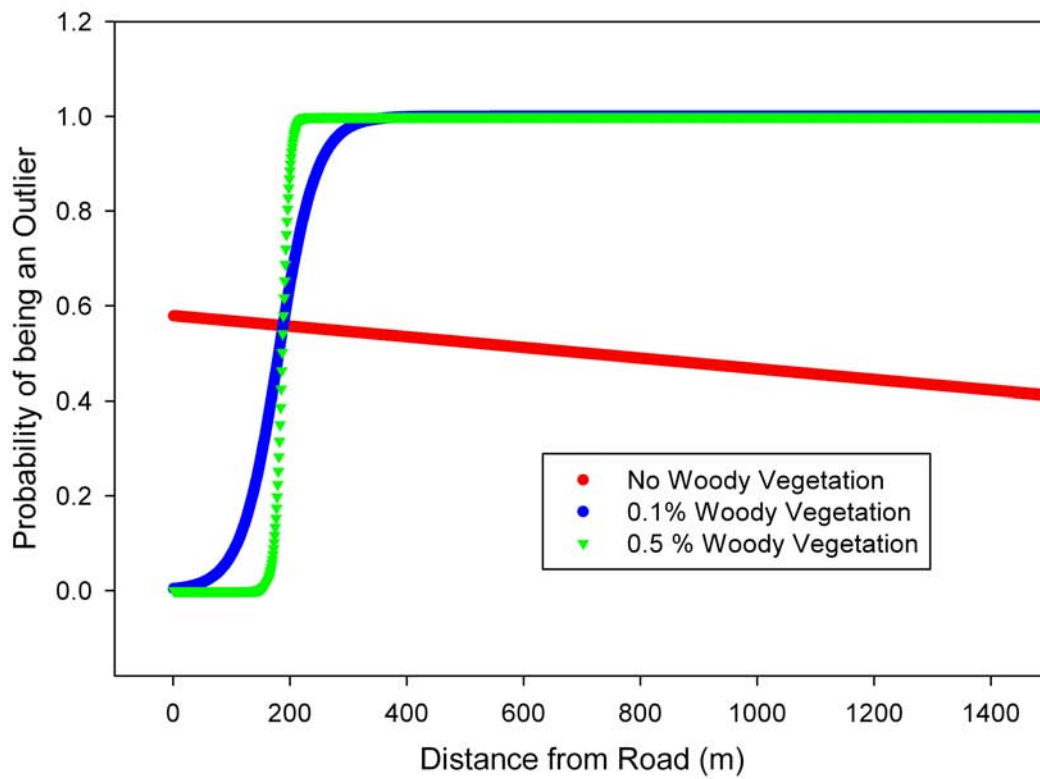


Figure B.7. Relationship between the distance to roads and the total amount of woody vegetation within a Savannah Sparrow territory at Last Mountain Lake in 2006 at the $\pm 6\%$ outlier classification.

Table B.1. Summary of models developed to explain Sprague's Pipit fidelity to an area based on habitat and landscape classifications at the $\pm 6\%$ outlier classification. All models are shown, as selected using AIC_c model selection. Data from Last Mountain Lake, SK, Canada, 2006.

K^c	Model	AIC_c	ΔAIC_c^a	w_i^b	R^{2 d}
1	null	80.0	0.0	0.44	-
2	Habitat	81.1	1.1	0.26	0.02
2	Landscape	82.1	2.0	0.16	0.00
3	Habitat, Landscape	83.2	3.2	0.09	0.02
4	Habitat, Landscape, Habitat*Landscape	84.8	4.8	0.04	0.03

^a ΔAIC_c = difference in AIC_c units between respective model and best model

^b Akaike weight

^c Number of parameters

^d Cox & Snell R Square

Table B.2. Summary of models developed to explain Sprague's Pipit fidelity to an area based on habitat and landscape classifications at the $\pm 10\%$ outlier classification. All models are shown, as selected using AIC_c model selection. Data from Last Mountain Lake, SK, Canada, 2006.

K^c	Model	AIC_c	ΔAIC_c^a	w_i^b	R²^d
1	null	88.0	0.0	0.51	-
2	Landscape	90.0	2.1	0.18	0.00
2	Habitat	90.1	2.1	0.17	0.00
4	Habitat, Landscape, Habitat*Landscape	91.6	3.6	0.08	0.05
3	Habitat, Landscape	92.2	4.3	0.06	0.00

^a Δ AIC_c = difference in AIC_c units between respective model and best model

^b Akaike weight

^c Number of parameters

^d Cox & Snell R Square

Table B.3. Summary of models developed to explain Savannah Sparrow fidelity to an area based on habitat and landscape classifications at the $\pm 10\%$ outlier classification. All models are shown, as selected using AIC_c model selection. Data from Last Mountain Lake, SK, Canada, 2006.

K^c	Model	AIC_c	ΔAIC_c^a	w_i^b	R^{2 d}
1	null	133.5	0.0	0.47	-
2	Landscape	134.9	1.4	0.24	0.01
2	Habitat	135.5	1.9	0.18	0.00
3	Habitat, Landscape	136.9	3.3	0.09	0.01
4	Habitat, Landscape, Habitat*Landscape	138.8	5.3	0.03	0.01

^a ΔAIC_c = difference in AIC_c units between respective model and best model

^b Akaike weight

^c Number of parameters

^d Cox & Snell R Square

Table B.4. Summary of models developed to explain Savannah Sparrow fidelity to an area based on habitat and landscape classifications at the $\pm 6\%$ outlier classification. All models are shown, as selected using AIC_c model selection. Data from Last Mountain Lake, SK, Canada, 2006.

K^c	Model	AIC_c	ΔAIC_c^a	w_i^b	R²^d
1	null	155.5	0.0	0.49	-
2	Habitat	157.1	1.6	0.22	0.00
2	Landscape	157.5	2.1	0.17	0.00
3	Habitat, Landscape	159.2	3.7	0.08	0.00
4	Habitat, Landscape, Habitat*Landscape	160.4	4.9	0.04	0.01

^a Δ AIC_c = difference in AIC_c units between respective model and best model

^b Akaike weight

^c Number of parameters

^d Cox & Snell R Square

Table B.5. Summary of models developed to explain Sprague's Pipit fidelity to an area based on habitat and landscape classifications at the $\pm 6\%$ outlier classification. All models with $\Delta AIC_c < 2$ are shown, as selected using AIC_c model selection. Data from Last Mountain Lake, SK, Canada, 2006.

K^c	Model	AIC_c	ΔAIC_c^a	w_i^b	R^{2 d}
4	TotWater89, TotTame89, TotWater89*TotTame89	76.5	0.0	0.23	0.15
4	TotWater89, TotNative89, TotWater89*TotNative89	76.7	0.2	0.20	0.15
4	DistR, TotTame1600, DistR*TotTame1600	77.6	1.1	0.13	0.14
2	TotWater89	78.4	1.9	0.09	0.06

^a ΔAIC_c = difference in AIC_c units between respective model and best model

^b Akaike weight

^c Number of parameters

^d Cox & Snell R Square

Table B.6. Summary of models developed to explain Sprague's Pipit fidelity to an area based on habitat and landscape classifications at the $\pm 10\%$ outlier classification. All models with $\Delta AIC_c < 2$ are shown, as selected using AIC_c model selection. Data from Last Mountain Lake, SK, Canada, 2006.

K^c	Model	AIC_c	ΔAIC_c^a	w_i^b	R^{2 d}
3	TotWater89, TotWood89	86.6	0.0	0.09	0.09
4	DistC, TotWood89, DistC*TotWood89	86.8	0.3	0.08	0.12
4	TotNative89, TotWood89, TotNative89*TotWood89	87.1	0.5	0.07	0.11
2	TotWood89	87.5	1.0	0.06	0.04
2	TotWater89	87.6	1.0	0.05	0.04
1	null	88.0	1.4	0.04	-
4	TotWater89, TotWood89, TotNative89	88.1	1.5	0.04	0.10
3	TotNative89, TotWood89	88.5	1.9	0.03	0.06

^a ΔAIC_c = difference in AIC_c units between respective model and best model

^b Akaike weight

^c Number of parameters

^d Cox & Snell R Square

Table B.7. Summary of models developed to explain Savannah Sparrow fidelity to an area based on habitat and landscape classifications at the $\pm 10\%$ outlier classification. All models with $\Delta AIC_c < 2$ are shown, as selected using AIC_c model selection. Data from Last Mountain Lake, SK, Canada, 2006.

K^c	Model	AIC_c	ΔAIC_c^a	w_i^b	R^{2 d}
1	null	133.5	0.0	0.10	-
2	TotWood1600	134.5	1.0	0.06	0.01
2	TotWater1600	134.6	1.1	0.06	0.01
4	DistR, TotNative56, DistR*TotNative56	134.9	1.4	0.05	0.04
2	TotWater56	135.3	1.8	0.04	0.00
2	TotNative56	135.3	1.8	0.04	0.00
2	TotTame1600	135.4	1.9	0.04	0.00
2	DistR	135.4	1.9	0.04	0.00
2	TotTame56	135.4	1.9	0.04	0.00
2	DistC	135.4	1.9	0.04	0.00

^a ΔAIC_c = difference in AIC_c units between respective model and best model

^b Akaike weight

^c Number of parameters

^d Cox & Snell R Square

Table B.8. Summary of models developed to explain Savannah Sparrow fidelity to an area based on habitat and landscape classifications at the $\pm 6\%$ outlier classification. All models with $\Delta AIC_c < 2$ are shown, as selected using AIC_c model selection. Data from Last Mountain Lake, SK, Canada, 2006.

K^c	Model	AIC_c	ΔAIC_c^a	w_i^b	R^{2 d}
4	DistR, TotWood56, DistR*TotWood56	148.9	0.0	0.40	0.11
5	DistR, TotWood56, TotWater56, DistR*TotWood56	150.4	1.5	0.19	0.12

^a ΔAIC_c = difference in AIC_c units between respective model and best model

^b Akaike weight

^c Number of parameters

^d Cox & Snell R Square

APPENDIX C: DERIVING YEAR- AND SITE-SPECIFIC FEATHER δD ISOSCAPES FOR ASSIGNING MIGRATORY BIRDS TO MOLT ORIGIN

C.1 Abstract

It is well established that precipitation amount weighted average deuterium (δD_p) shows substantial inter-annual variation. More specifically, local growing-season δD_p at locations within the Great Plains of North America deviate from that described by current interpolated GIS-based models of stable hydrogen isotope ratios in North America derived from long-term estimates of growing-season precipitation and the long-term average monthly deuterium in precipitation. I augmented the GNIP dataset with information from the USNIP database for sites in the Great Plains and developed a method of correcting the Bowen et al. (2005) isoscape. By accounting for longitude and the coefficient of variation within precipitation in a single year at a specific location, I determined a year- and site-specific best estimate of δD_p . This method of determining local growing-season δD_p is an improvement upon the Bowen et al. (2005) isoscape, as it more closely predicted the deuterium in feathers (δD_f) of known-source Sprague's Pipit feathers grown at Last Mountain Lake in 2004 and 2005. Future research involving the assignment of individuals to origins based on their δD_f values should incorporate year to year variation by applying year-specific corrections of the Bowen et al. (2005) isoscape for improved assignment of individuals of unknown origins.

C.2 Introduction

In recent years, the use of stable hydrogen isotope ratios (δD) has become a widely used tool for studying large-scale movements of migratory organisms, particularly birds (Hobson and Wassenaar 1997, Wassenaar and Hobson 2000, Paxton et al. 2007). This approach takes advantage of geographically predictable patterns in the isotopic composition of rainfall that are

driven by factors such as climate, latitude, and altitude (Dansgaard 1964). In North America, the precipitation-amount weighted average δD (hereafter δD_p) typically decrease in a northwesterly fashion, with the most positive values occurring near the equator. Stable isotopes in precipitation are transferred to local foodwebs and subsequently reflected in the tissues of organisms feeding within those foodwebs (Hobson 1999). Numerous studies have shown that the isotopic composition of a particular animal tissue reflect those in local dietary inputs, with some minor discrimination between trophic levels (Wassenaar and Hobson 2000). As organisms move between isotopically distinct foodwebs, they carry with them information on the previous feeding location (Hobson 1999). In the case of migratory songbirds, most species grow their flight feathers on or near the breeding grounds (Pyle 1997), allowing the approximate latitude of their breeding grounds to be determined using δD analysis of the flight feathers (Hobson 1999).

In order for δD analysis to be an effective tool for studying migration, it is important to be able to reliably assign individuals to the correct location of feather growth. The accuracy of assigning feathers of unknown origin spatially may be complicated by several factors, such as sampling and analytical error, inter-individual variation in physiology, and uncertainty associated with spatially interpolated isoscapes to which samples are being assigned (Wunder and Norris 2008). Previously, it was common to assign individuals to an associated geographic range by defining those regions of isoscapes consistent with the tissue value measured. This “map lookup” approach (Wunder and Norris 2008) is intuitively appealing but does not formally propagate error associated variance in tissue isotope values at a given location.

Precipitation isoscapes are typically generated from spatial patterns in δD caused by indirect sources (e.g. rainfall). Typically, isoscapes used to assign individuals of unknown origin are of calibrated feather δD values (hereafter δD_f) values by regression of δD_f values against isoscape-

predicted values of δD_p , using samples of known origin (Hobson et al. 1999). Briefly this process involves establishing δD_p values for locations with δD_p sampling stations. The δD_p values for locations between sampling stations are interpolated using kriging, creating a surface of δD_p values. Using a regression derived from Clark et al. (2006, see Equation C.2), δD_p values are converted to δD_f values, resulting in an isoscape of δD_f values. Ideally, isoscapes will be calibrated for each species using known origin tissues (gathered from the same species, age class and habitats as the samples of interest) that were collected from across the full extent of the geographic range and during the same years as the samples of interest (Wunder and Norris 2008). However, in most cases, these data are unavailable. Therefore, the next best approach would be to use published isoscapes and regression coefficients that correspond most closely to the species and geographic range of interest.

One of the most useful isoscapes for assigning individuals to origin globally has been developed by Bowen et al. (2005). Bowen et al. (2005) constructed both annual and growing-season precipitation isoscapes using water isotope data from the Global Network of Isotopes in Precipitation (GNIP) database. Bowen et al. (2005) created isoscapes of monthly mean deuterium (δD_p) and oxygen ($\delta^{18}O_p$) in precipitation, using a modification of a previously described detrended interpolation method for mean annual δD_p and $\delta^{18}O_p$ (Bowen and Wilkinson 2002, Bowen and Revenaugh 2003). This method treats the isotopic composition of precipitation as the sum of temperature-driven rainout effects and regional patterns of vapor sourcing and delivery (Bowen and Wilkinson 2002). Bowen et al. (2005) weighted the monthly δD_p surfaces with interpolated long-term precipitation to derive a weighted growing season (defined as all months with an average temperature $>0^\circ\text{C}$) δD_p surface.

There are several important limitations to the use of isoscapes derived from the GNIP database. First, the spatial distribution of sampling locations is variable and there are large areas of the continent with limited or no sampling. Secondly, the GNIP database represents a compilation of data that was collected over 40 years, but data for all years is not available at all sampling locations, and in many localities data are no longer collected. Furthermore, isoscapes derived from the GNIP data set are derived using long-term averages of monthly δD . In addition, isoscapes of growing-season δD are typically generated by weighting measurements of δD in precipitation by the long-term average amount of precipitation in the months contributing to the growing season (Hobson and Wassenaar 1997; Bowen et al. 2005) and therefore may not accurately capture the amount of inter-annual variation possible in some localities. Recent work (Farmer et al. 2008), suggests that inter-annual variance at GNIP stations may be an important factor limiting the geographic precision to which migratory animals can be assigned to their origins. However, Farmer et al. (2008) did not use precipitation-averaged GNIP data. Therefore it is flawed and it is not yet clear what the fundamental limits are to the accuracy and precision of δD based assignment of spatial origins for migratory birds.

Despite limitations to the use of δD isoscapes, the application of these isoscapes has still been extremely successful (Hobson et al. 2006, Lott and Smith 2006, Hobson et al. 2007, Paxton et al. 2007). However, there may be room for further refinement of δD isoscapes. In particular, year-specific δD isoscapes may reduce the uncertainty in assigning samples to their origins, particularly for regions with high inter-annual variance in δD in precipitation. I augmented the GNIP data with other δD_p data and examined parameters causing inter-annual variation.

Objective:

To derive improved δD_p isoscapes using year- and site-specific data within the North American Great Plains, using the Sprague's Pipit breeding range as an example.

C.3 Methods and Study Design

I acquired δD_p data for eight sites within the North American Great Plains from both the GNIP dataset and the United States Network of Isotopes in Precipitation (USNIP, J. Welker, unpublished data) dataset. The USNIP dataset constitutes an effort to provide $\delta^{18}O$ and δD isotopic values for ~80 sites across the United States using National Atmospheric Deposition Program (NADP) sampling stations. The eight sites included Saskatoon (SK), Wynyard (SK), Edmonton (AB), Calgary (AB) and Esther (AB), Cottonwood (SD), Glacier National Park –Fire Weather Station (MT) and Little Bighorn Battlefield National Monument (MT) (Figure C.1). For these sites, I also acquired monthly precipitation and temperature data from the Canadian Climate Center (Environment Canada 2005) and the Western Regional Climate Center (Western Regional Climate Center 2008).

Using these precipitation and temperature data, I calculated year-specific local weighted growing-season δD_p values (hereafter δD_{p-gs}) for each site. I compared year-specific δD_{p-gs} to the δD_{p-gs} predicted by the Bowen et al. (2005) isoscape (hereafter δD_{Bowen}), to determine how δD_{p-gs} deviates from the Bowen et al. (2005) isoscape between years. Precipitation and temperature variables were assessed because latitude, altitude and seasonal air-mass trajectories result in predictable patterns of precipitation and temperature (Bowen et al. 2005). I calculated the following year-specific explanatory variables: the year-specific growing-season percent deviance in precipitation from the long term average growing-season precipitation, total growing-season precipitation, mean growing-season precipitation and the coefficient of variation in precipitation

during the growing season. The coefficient of variation in precipitation was included as an explanatory variable as I assumed it may reflect differences among years in convectively generated versus frontal system generated precipitation. All precipitation values are based on growing-season precipitation because grasslands respond more readily to short-term rainfall events (Sala and Lauenroth 1982). I also included mean growing-season temperature as a candidate explanatory variable. I predicted these variables may all have some affect on how the year-specific δD_{p-gs} deviates from the values predicted by the Bowen et al. (2005) isoscape. Longitude was also included because it is not accounted for in the Bowen et al. (2005) isoscape. Furthermore, longitude may accurately reflect rain-shadow effects associated with the Rocky Mountains. Growing season was site-specific and was defined as all months at that site with an average temperature $>0^{\circ}\text{C}$.

C.4 Statistical Analysis

I determined a candidate set of best models, excluding all correlated variables. This candidate set included longitude (Long), average growing-season temperature (Ave GS Temp) and the coefficient of variation in precipitation (CVprecip). Linear regression was conducted on this candidate set of best models with the dependant variable being the deviance of the year- and site-specific δD_{p-gs} from the δD_{Bowen} . I used Akaike's Information Criterion (adjusted for small sample size, AIC_c ; Burnham and Anderson 2002) to select among seven candidate models. These models included a null model, longitude, average growing-season temperature and the coefficient of variation within precipitation as main effects models, as well as all subsets of additive models including two variables. The most parsimonious model was considered to be that with the lowest AIC_c value. All models with a ΔAIC_c value < 2 were considered supported by



Figure C.1. GNIP and USNIP station locations within the Great Plains of North America.

the data (Burnham and Anderson 2002). Akaike model weights were calculated to determine the weight of evidence that a given model was the best model of those I considered (Burnham and Anderson 2002).

C.5 Isoscape Creation

Monthly growing-season precipitation data for sites within the Canadian Great Plains were acquired for 2002 through 2006 (Environment Canada 2005, Western Regional Climate Center 2008). Using these data, coupled with the algorithm derived from AIC_c model selection, I calculated year- and site-specific δD_{p-gs} values from locations across the Canadian Great Plains. From these, I created year-specific isoscapes showing the amount of deviance in δD_{p-gs} from δD_{Bowen} in the Great Plains using ArcMap9.3 (ESRI Inc. 2008).

C.6 Results

C.6.1 Algorithm

Year-specific deviations in δD_{p-gs} from the Bowen et al. (2005) isoscape were strongly influenced by longitude and variation in precipitation (Table C.1). The model including longitude and the coefficient of variation of precipitation was the most parsimonious model of all the models considered ($w_i = 0.81$). This model explained approximately 42% of the variance in the data; no other models were considered supported by the data (Table C.1). Deviance from the Bowen et al. (2005) isoscape increased from west to east (Figure C.2) and with increasing variation in precipitation (Figure C.3). Based on this model, the algorithm to estimate departures from δD_{Bowen} at specific sites and years is as follows:

Table C.1. Summary of models developed to explain variables that cause year-specific deviances in the δD_{p-gs} from the δD_{p-gs} predicted by the Bowen et al. (2005) isoscape. All models are shown. Data from the Great Plains of North America ($n = 39$).

K^c	Model	AIC_c	ΔAIC_c^a	w_i^b
4	Long, CVprecip	198.8	0.0	0.81
3	Long	203.4	4.6	0.08
4	Long, Ave GS Temp	203.4	4.6	0.08
4	CVprecip, Ave GS Temp	207.4	8.6	0.01
3	CVprecip	207.8	9.0	0.01
3	Ave GS Temp	211.8	13.0	0.00
2	null	215.1	16.6	0.00

^a ΔAIC_c = difference in AIC_c units between respective model and best model

^b Akaike weight

^c Number of parameters

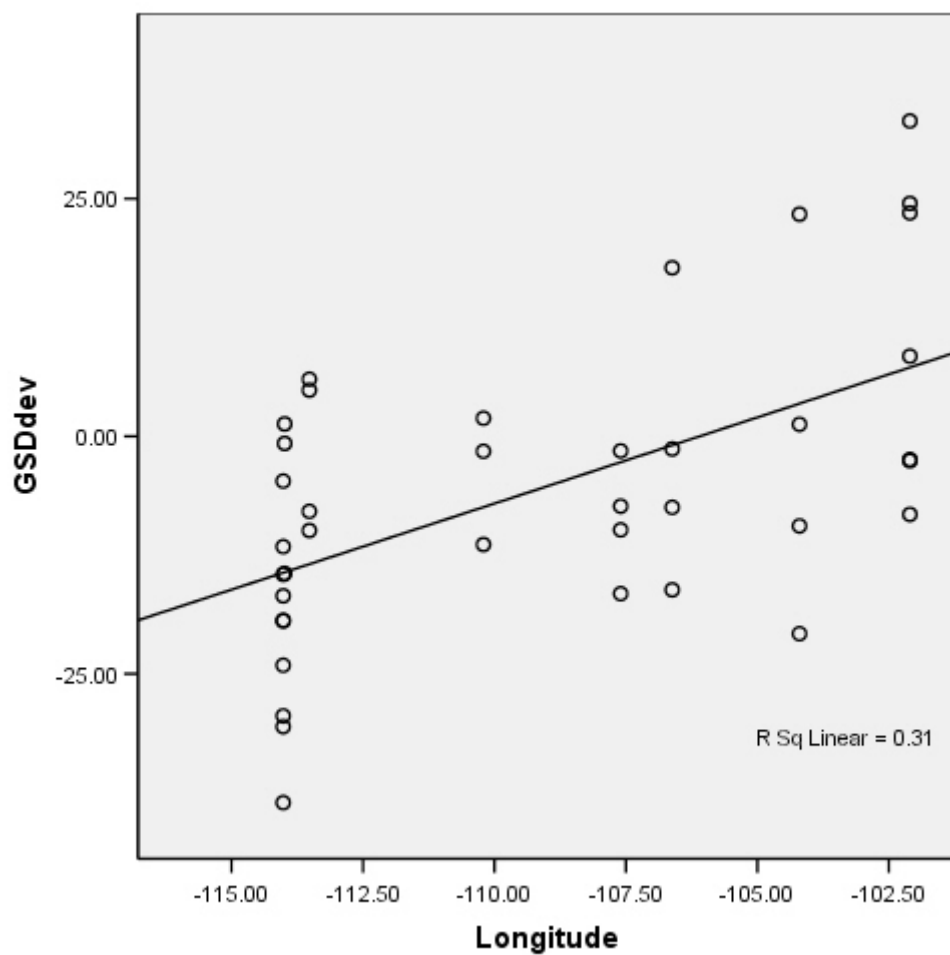


Figure C.2. Relationship between the deviance in δD_{p-gs} from the Bowen et al. (2005) isoscape and the raw longitudinal data.

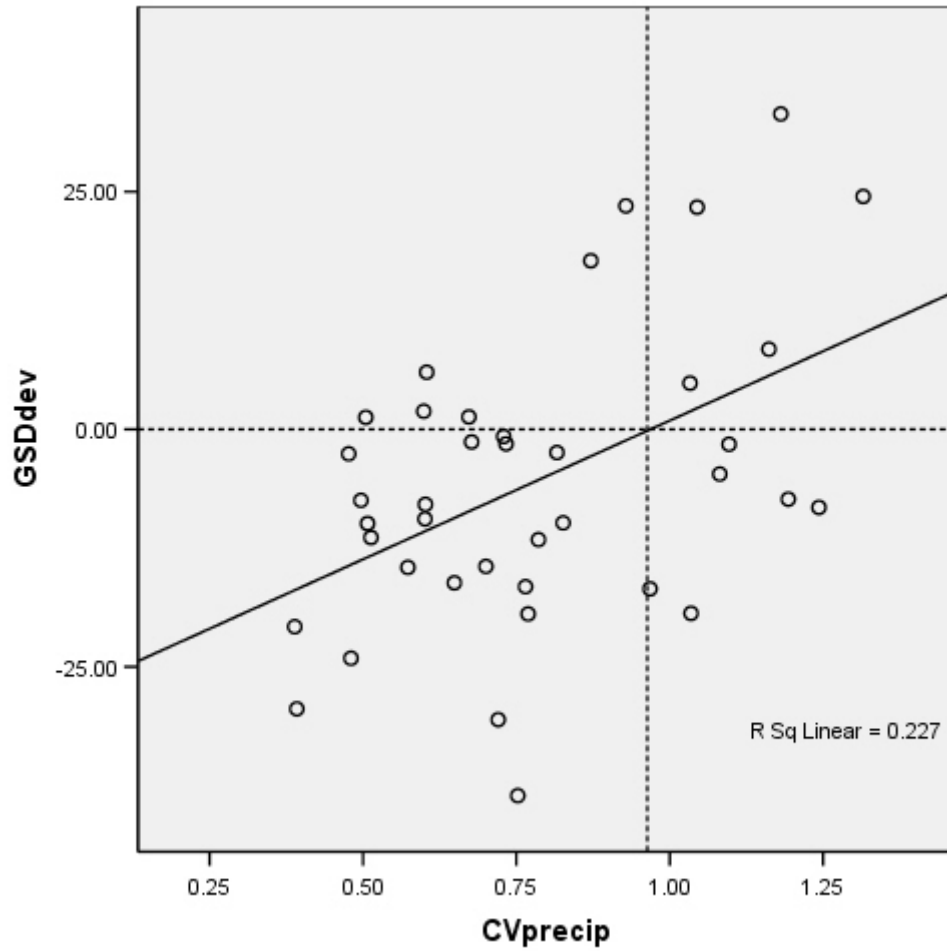


Figure C.3. Relationship between the deviance in δD_{p-gs} from the Bowen et al. (2005) isoscape and the raw coefficient of variation in precipitation data. Dashed lines indicate the coefficient of variation in precipitation ($CV_{precip} = 0.96$) of the long-term average precipitation data depicted in the Bowen et al. (2005) isoscape for the Great Plains of North America.

$$\text{Deviance from } \delta D_{\text{Bowen}} = 141.68 + 1.50 * (\text{Long}) + 21.54 * (\text{CVprecip}) \quad (\text{C.1})$$

I used this algorithm to calculate the year-specific predicted $\delta D_{\text{p-gs}}$ at locations within the Great Plains.

C.6.2 Inter-annual Variation

Extensive inter-annual variation was evident at locations within the North American Great Plains (Figure C.4). At Cottonwood, Edmonton and Saskatoon, inter-annual variation in four consecutive years ranged from -89‰ to -48‰, -124‰ to -108‰ and -121‰ to -87‰, respectively. Years with more variation within precipitation experienced more enriched values than was predicted by Bowen et al. (2005), while years with less variation experience more depleted values. In either case, δD_{Bowen} was a good estimation, but failed to capture the variation among years.

C.6.3 Isoscape Creation

I determined year- and site-specific deviances in $\delta D_{\text{p-gs}}$ from the δD_{Bowen} predicted by the Bowen et al. (2005) isoscape using the algorithm described above (Equation C.1). I created year-specific interpolated maps (ArcMap 9.3, ESRI Inc. 2008) of deviances in $\delta D_{\text{p-gs}}$ from δD_{Bowen} (Figure C.5). From these, I acquired year-specific corrections for the Bowen et al. (2005) isoscape, specifically for Last Mountain Lake and Bowdoin National Wildlife Refuge study areas (Table C.2), thereby deriving corrected $\delta D_{\text{p-gs}}$ values for these locations. These $\delta D_{\text{p-gs}}$ values were converted to δD_{f} values using the following regression derived from the Clark et al. (2006) data:

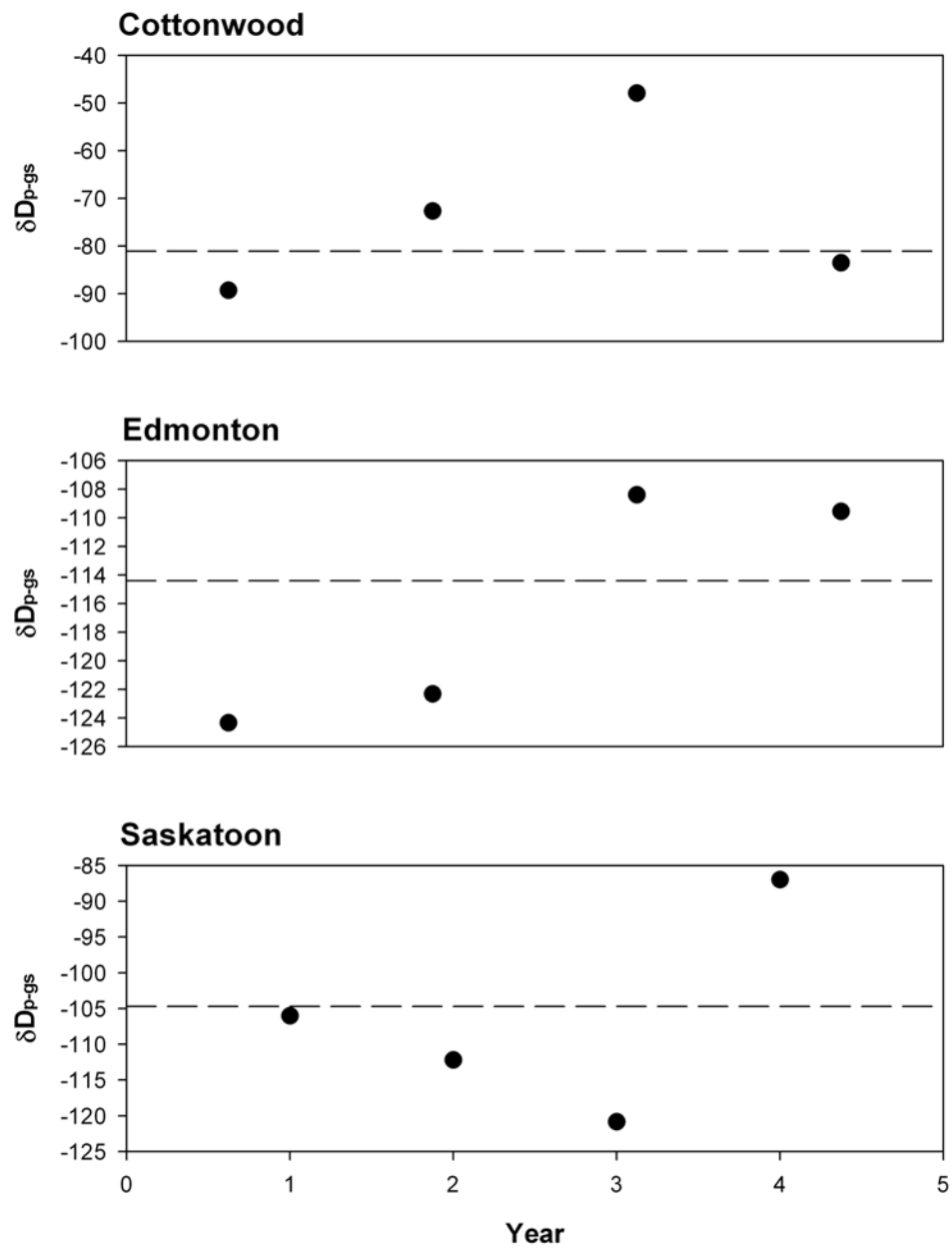


Figure C.4. Year to year variance in δD_{p-gs} over four consecutive years at three locations within the North American Great Plains. The dashed line indicates δD_{Bowen} predicted by the Bowen et al. (2005) isoscape.

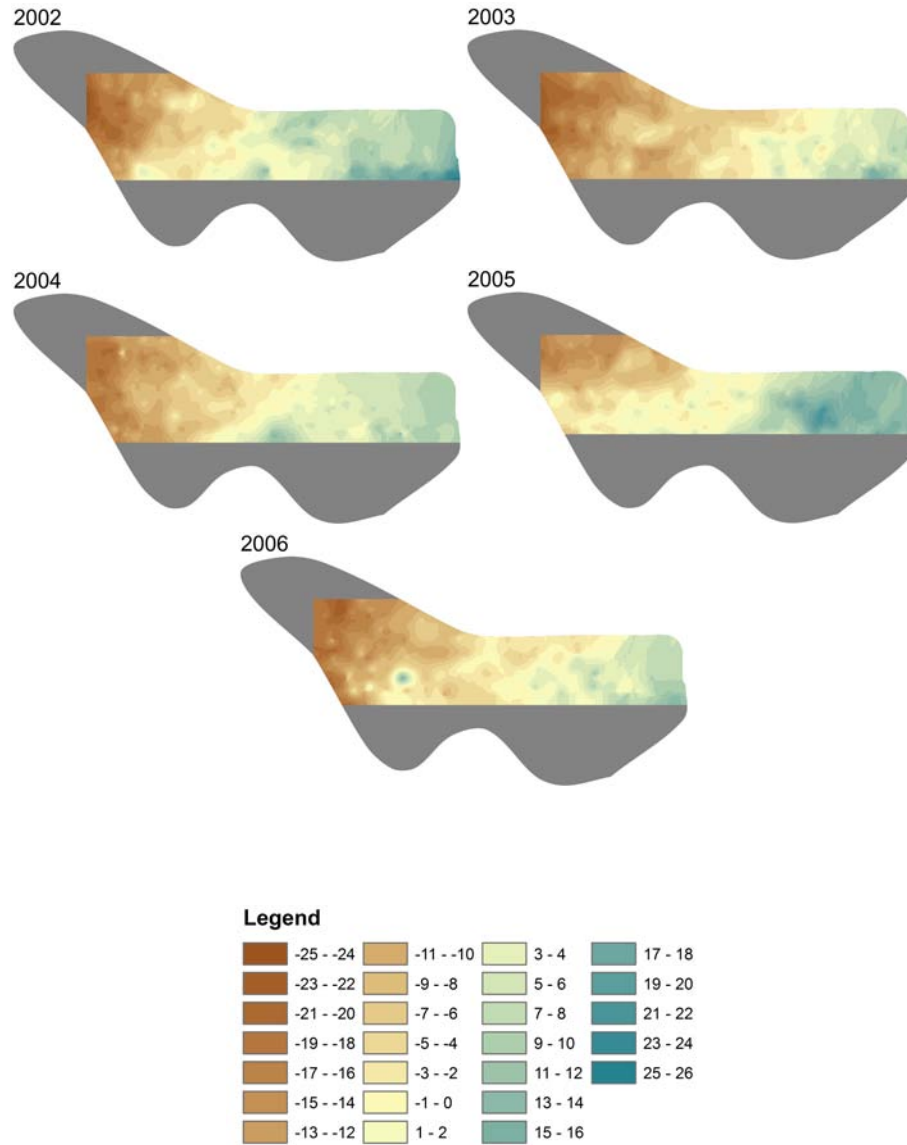


Figure C.5. Year-specific kriged maps of deviances in the calculated δD_{p-gs} from the δD_{Bowen} predicted by the Bowen et al. (2005) isoscape. The area indicated is the Sprague's Pipit breeding range, with grey regions having no available data. Values indicate the permil (‰) deviation from the Bowen et al. (2005) isoscape.

Table C.2. Year-specific δD_{p-gs} and δD_f values for Last Mountain Lake, SK and Bowdoin National Wildlife Refuge, MT.

Site	Year	Bowen et al. (2005) δD_{p-gs}	Bowen et al. (2005) δD_f	Year-specific δD_{p-gs}	Year-specific δD_f
Last Mountain Lake, SK	2002	-102	-116	-93	-108
	2003	-102	-116	-107	-120
	2004	-102	-116	-101	-115
	2005	-102	-116	-99	-113
	2006	-102	-116	-106	-119
Bowdoin National Wildlife Refuge, MT	2002	-94	-108	-93	-108
	2003	-94	-108	-99	-114
	2004	-94	-108	-95	-109
	2005	-94	-108	-90	-105
	2006	-94	-108	-101	-115

$$\delta D_f = -26.08 + 0.88(\delta D_{p-gs}) \quad (C.2)$$

These δD_f values are the best estimate of the expected δD_f value of a feather grown at these locations in these years and were used to compare to all captured individuals' δD_f values to determine if the individual was a returning or non-returning breeder.

To test the ability of our algorithm to better predict the expected δD_f of a feather grown at a specific location, I compared the calculated year-specific δD_f values at Last Mountain Lake to the δD_f values of Sprague's Pipit feathers that were known to have been grown at Last Mountain Lake in those years. In 2005, two Sprague's Pipits were captured that were known to have grown their feathers at Last Mountain Lake in 2004. The first individual had a fourth rectrix δD_f value of -112‰. The second individual had δD_f values of -112‰ from the sixth primary and -118‰ from the fourth rectrix. Although the fourth rectrix of one individual is better predicted by the Bowen et al. (2005) isoscape δD_f value (-116‰), the sixth primary of that individual and the fourth rectrix of the other individual are better predicted by the 2004-specific δD_f value (-115‰). In 2006, a single Sprague's Pipit was captured that was known to have grown its feathers at Last Mountain Lake in 2005. This individual had a fourth rectrix δD_f value of -111‰. As with the previous cases, the observed δD_f is better predicted by the 2005-specific δD_f value (-113‰) than the Bowen et al. (2005) isoscape δD_f value (-116‰). Unfortunately, there were no known-source Sprague's Pipits captured at the Bowdoin National Wildlife Refuge.

C.7 Discussion

C.7.1 Importance of Correcting for Year

It is well established that δD_p shows substantial inter-annual variation (Wunder et al. 2005), particularly in the Great Plains of North America, which experiences highly variable precipitation and temperature (Borchert 1950, Bryson and Hare 1974). It is not clear why the

coefficient of variation within precipitation is driving the most parsimonious model. However, it is possible that years with increased variation among months could be attributed to convectively-generated precipitation events. Convectively-generated precipitation events are evaporation driven (Bowen and West 2008), causing an overall enrichment of the plant δD value, which ultimately drives δD_f . In contrast, a low coefficient of variation could be experienced by either consistently hot, dry conditions or consistently cool, wet conditions. However, it seems that in the Great Plains, a low coefficient of variation was accompanied by more depleted (compared to the long-term average) δD values (Figure C.3) and therefore I speculate that when there is a low coefficient of variation, the area experienced consistently cool, wet conditions. Given this substantial inter-annual variation, it is likely that there may also be large variations in δD_f between years, though perhaps not as drastic as in precipitation due to attenuation of variance in higher trophic levels (Bump et al. 2007). Although the Bowen et al. (2005) isoscape is an excellent starting point when trying to determine the expected δD_{p-gs} value for a specific location, accounting for the variance in δD_{p-gs} between years is essential. Year to year variance can be extensive (Figure C.4 and C.5) and an individual can easily be incorrectly assigned due to discrepancy between years if this variation is not considered.

By refining our best estimate of δD_{p-gs} by both site and year, we are one step closer to determining a more accurate estimate of δD_{p-gs} . An accurate estimate of δD_{p-gs} , coupled with a precise regression equation with which to convert δD_{p-gs} values to δD_f values, will allow more reliable estimates of the origin of an unknown-source individual given its δD_f value. In short, accounting for the year should improve the ability to assign individuals to a location of origin.

C.7.2 Uses of Corrected Isoscape Maps

The most fundamental use of corrected isoscape maps will be the improved ability to assign individuals to a location of origin. Within the Great Plains of North America, researchers now have an algorithm that can be used to determine year-specific estimates of δD_{p-gs} for a site of interest. By using the regression derived from Clark et al. (2006) to convert δD_{p-gs} values to δD_f values, researchers can now more accurately estimate the expected δD_f value at a specific location within a specific year. This will improve our ability to determine if an individual of unknown origin indeed originated from the location of interest, which also has implications for assessing the number of long-range dispersers within a population (see Hobson et al. 2004)

Furthermore, this tool can be used to create year-specific isoscapes of an area within the Great Plains, rather than simply a year-specific estimate of a single site. This would improve the ability to assign an individual to a location of origin by allowing an individual that may have not originated at a specific location of interest to then be assigned to another location within the isoscape. Ultimately, the researcher now has the ability to determine an estimate of $\delta D_{p-gs} / \delta D_f$ not only for their area of interest, but also the time frame of interest.

Although I have only created a corrected isoscape for the northern extent of the Sprague's Pipit breeding range at this time, arguably this technique could be applied to a broader scale. In order to extend the application of the approach used herein, I would suggest more GNIP and USNIP sampling locations be incorporated. In this case, only eight sites were used, as sites were limited to those within the Great Plains of North America for which more or less complete temporal δD data for a minimum of three years was available. However, broader scale isoscapes could include analysis of a broader suite of GNIP and USNIP sampling locations.

C.8 Conclusion

I have presented a tool that should decrease uncertainties in assignment of individuals to origin due to inter-annual variation in the δD_{p-gs} at spatially explicit locations. This tool provides an improvement on the Bowen et al. (2005) isoscape, as demonstrated by the comparison of known-source feathers of Sprague's Pipits and the estimated δD_f value for that location in the year of growth. The addition of more known-source birds from within the Northern Great Plains would greatly aid in further assessing the strengths and/or weaknesses of the approach taken here. Future research involving the assignment of individuals to origins based on their δD_f values should consider applying year-specific corrections of the Bowen et al. (2005) isoscape for improved assignment.

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APPENDIX D: SUPPLEMENTAL FIGURES AND TABLES FROM CHAPTER 3



Figure D.1. Study site locations within the Great Plains of North America. Blue area indicates the Sprague's Pipit breeding range derived from Breeding Bird Survey Data from 1985 – 1991.

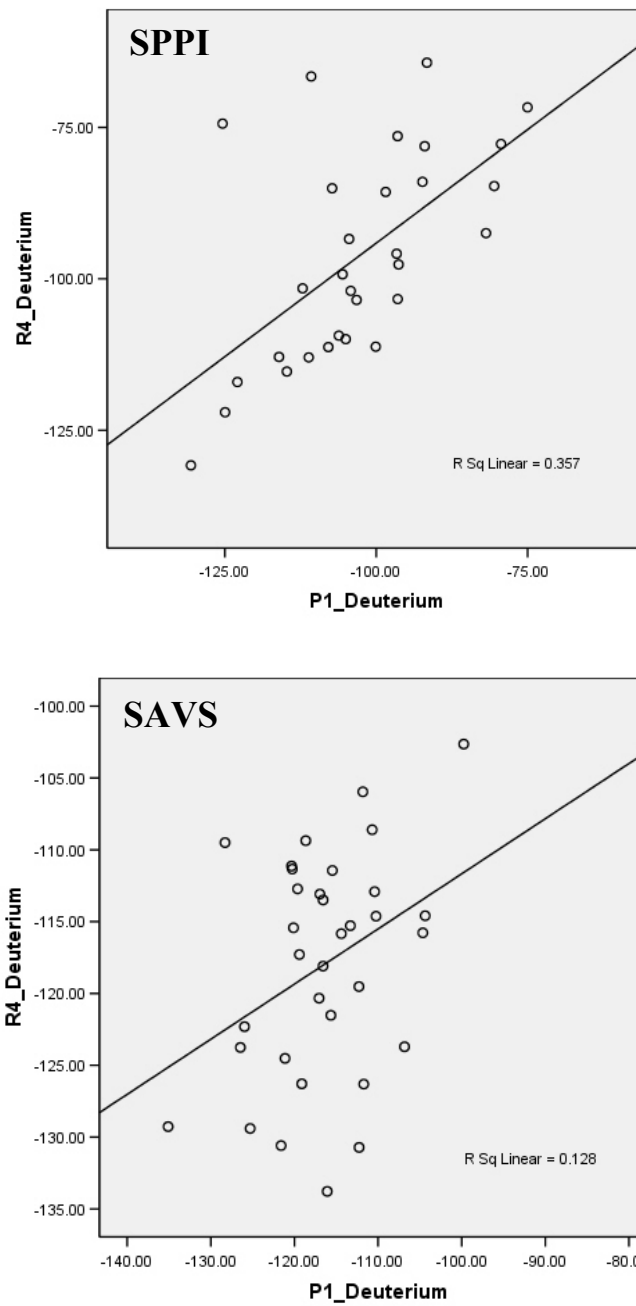


Figure D.2. Correlation between the δD_f of the first primary feather (P1) and the fourth rectrix (R4) for Sprague's Pipit (SPPI) and Savannah Sparrow (SAVS).

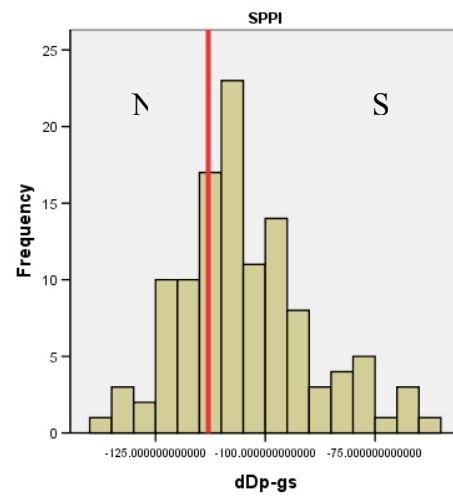
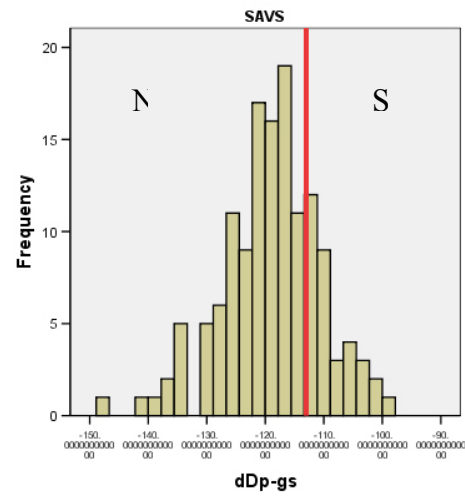


Figure D.3. Histogram of SAVS and SPPI individuals caught at LML in 2006. North (N) and south (S) are indicated, as well as the LML δD_f value representing individuals captured in 2006.

Table D.1. Z-test of proportions of outliers captured in the Last Mountain Lake National Wildlife Area versus outside the National Wildlife Area for individuals caught at Last Mountain Lake, SK, Canada. Sprague's Pipit (SPPI) and Savannah Sparrow (SAVS) and outlier classification ($\pm 10\%$ or $\pm 6\%$) are indicated in parenthesis. The critical z-value is 2.25 (after applying a Bonferonni correction).

Comparison	Z- value
NWA data vs Non NWA data (SAVS, $\pm 10\%$)	0.24
NWA data vs Non NWA data (SAVS, $\pm 6\%$)	-0.18
NWA data vs Non NWA data (SPPI, $\pm 10\%$)	-0.66
NWA data vs Non NWA data (SPPI, $\pm 6\%$)	0.36